ECTOPARASITES OF THE HAWAIIAN ISLANDS

I. SIPHONAPTERA[1]

By

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ABSTRACT

The following 10 species of fleas are considered established in the Hawaiian Islands: *Echidnophaga gallinacea, Pulex irritans, P. simulans, Ctenocephalides felis felis, C. canis, Xenopsylla cheopis, X. vexabilis, Parapsyllus laysanensis* Wilson, n. sp., *Nosopsyllus fasciatus*, and *Leptopsylla segnis*. Two additional species, *Polygenis gwyni* and *Monopsyllus anisus*, of apparently accidental occurrence, are treated briefly. The account of each species includes: synonymy in Hawaii, records, history of introduction and establishment, ecological distribution, sex ratio, and hosts. A key and illustrations are provided to the species.

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[1]Supported in part by Public Health Service Research Grant No. AI-02886 from the National Institute of Allergy and Infectious Diseases to the Department of Health, State of Hawaii.

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Photo by John Shouse

Frontispiece.—*Parapsyllus laysanensis* Wilson, n. sp. Male holotype x 55.

CONTENTS

INTRODUCTION 4
ACKNOWLEDGMENTS 5
SYSTEMATICS 9
Key to the species 9
Pulicidae 10
1. *Echidnophaga gallinacea* 10
2. *Pulex irritans* 12
3. *Pulex simulans* 14
4. *Pulex* sp. 15
5. *Ctenocephalides felis felis* 15
6. *Ctenocephalides canis* 19
7. *Xenopsylla cheopis* 20
8. *Xenopsylla vexabilis* 23
Rhopalopsyllidae 31
9. *Parapsyllus laysanensis* Wilson, n. sp. 31
Ceratophyllidae 33
10. *Nosopsyllus fasciatus* 33
Leptopsyllidae 35
11. *Leptopsylla segnis* 35
LITERATURE CITED 38
APPENDIX 46
A. Names of hosts 46
B. Host synonymy 46
SOURCES OF FIGURES 47
INDEX 72

TABLES

1. Distribution of Hawaiian Siphonaptera 7
2. Host associations of Hawaiian Siphonaptera 8
3. *Xenopsylla vexabilis* populations in *Rattus exulans* and *Mus musculus* nests of different ages 30

FIGURES

1. Map of the Hawaiian Archipelago 6
2-4. *Echidnophaga gallinacea* 49
5-7. *Pulex irritans* 51
8-9. *Pulex irritans* 53
10. *Pulex simulans* 53
11-14. *Ctenocephalides felis felis* 55
15-18. *Ctenocephalides canis* 57
19-22. *Xenopsylla cheopis* 59
23-27. *Xenopsylla vexabilis* 61
28-30. *Parapsyllus laysanensis* Wilson, n. sp. 63
31. *Parapsyllus laysanensis* Wilson, n. sp. 65
32. *Parapsyllus taylori* 65
33. *Parapsyllus laysanensis* Wilson, n. sp. 67
34. *Parapsyllus taylori* 67
35-37. *Nosopsyllus fasciatus* 69
38-40. *Leptopsylla segnis* 71

INTRODUCTION

Fleas have been established in Hawaii for many hundreds of years, although most species are obviously modern introductions. The first person to indicate their presence appears to be Campbell (1816), who resided in Honolulu in 1809 and 1810. Numerous authors subsequently commented on fleas as pests (see historical account by Haas et al., 1971) without specifically identifying them. The first applications of a scientific name to a flea (as *Ctenocephalus canis*) are in the 1907 reports by Van Dine (1908) and Van Dine and Nörgaard (1908). By 1907 all present members of the fauna except *Echidnophaga gallinacea* probably were established. Consequently, we cannot refer to documented accounts of the early history of most species. Since 1908 a large quantity of literature on fleas in the Hawaiian Islands has accumulated, mostly because of the public health and veterinary importance of certain species.

Twelve species are recorded, 10 of which are established on at least one of the islands. One of the 10 species is endemic and described as new, one arrived with the Polynesians, and the others are cosmopolitan species of recent introduction. The 10 established species represent four families and seven genera. Of the 12 species, *Rhopalopsyllus* (= *Polygenis*) *gwyni* C. Fox possibly was recorded through an error (Cole and Koepke, 1947b). This species could have been introduced but failed to become established. In the flea collection of the Hawaiian Sugar Planters' Association (Honolulu) is a female *Monopsyllus anisus* (Rothschild) found in Honolulu in a packing case from Japan, October 1932, by Q. C. Chock. *M. anisus* was an immigrant from the Orient that failed to become established. If the specimen had been inseminated and deposited with *Rattus rattus* or *Rattus norvegicus* on one of the higher mountains, the Hawaiian Islands might have had an addition to its flea fauna. The two species of *Rattus* mentioned above are common hosts in Japan (Sakaguti, 1962, Sakaguti and Jameson, 1962). At least two specimens of *M. anisus* were recovered on the Pacific Coast of North America, in San Francisco and Vancouver (Mitzmain, 1909, Rothschild, 1910, Johnson, 1961).

In this era of greatly increased speed and volume of transportation, introduction of additional species of fleas into the islands is likely. They could arrive easily on small mammals such as those intercepted in recent years by quarantine personnel (Joyce, 1968). Establishment of a resident population may be difficult, but it is not impossible for some fleas despite loss of their true host. The cat flea-rabbit association recently discovered on Manana Island by Tomich et al., (1968) is a prime example of a recently developed flea-host relationship.

This monograph includes a compilation and summarization (Tables 1, 2) of published records of fleas including a few that are questionable because of the recent discovery that *Pulex* includes both *P. irritans* and *P. simulans* (Haas and Wilson, 1967). In addition, some early authors confused *Ctenocephalides felis* with *Ctenocephalides canis* and failed to distinguish *Xenopsylla vexabilis* from *Xenopsylla cheopis*. Among hosts, *Rattus exulans* was thought to be *R. norvegicus*.

In referring to the level of host specificity, we use the terms true host, secondary host, and accidental host after Sakaguti and Jameson (1962). Rainfall and other climatic data are from Blumenstock and Price (1967). Seasonal terms not used according to the definitions therein are placed in quotation marks.

Most specimens recorded in this paper were identified, then triturated in tests for plague. Other specimens were deposited in collections including those of the Bernice P. Bishop Museum, Honolulu; British Museum (Natural History), London; Field Museum of Natural History, Chicago; and the authors.

ACKNOWLEDGMENTS

We are grateful to Dr. C. M. Wheeler for his interest, encouragement, and assistance; R. H. Baker for loaning personnel to collect fleas from nests and small mammals; Drs. J. M. Klein and R. Traub for comments on *X. vexabilis*; F. G. A. M. Smit for confirming our determination of *C. canis* and comments on *Parapsyllus laysanensis*; Dr. E. W. Jameson, Jr. for confirming our determination of *M. anisus* and review of the manuscript; Dr. G. P. Holland for review of the manuscript; F. A. Bianchi and Dr. C. R. Joyce for loaning specimens under their care; Dr. R. L. Wenzel for assistance in obtaining literature; Dr. R. L. Pyle for allowing us to collect and record specimens from vertebrates belonging to the Smithsonian Pacific Ocean Biological Survey Program; Dr. W. O. Wirtz II for unpublished data from his studies of *R. exulans*; and Mrs. E. Snyder for typing the manuscript for photo-offset printing.

FIG. 1. MAP OF THE HAWAIIAN ARCHIPELAGO

Table 1. Distribution of Hawaiian Siphonaptera

Siphonaptera	Island[1] Laysan	Kauai	Oahu	Manana	Molokai	Lanai	Maui	Hawaii	Other localities
Pulicidae									
1. Echidnophaga gallinacea		X	X	X	X		X	X	Widespread in the tropics and subtropics; occasional in some cooler regions
2. Pulex irritans			?				?	X	Cosmopolitan
3. P. simulans		X	X				?	X	Nearctic and Neotropical Regions
4. Pulex sp.		X						X	
5. Ctenocephalides felis felis		X	X	X	X	X	X	X	Cosmopolitan
6. C. canis			?					X	Cosmopolitan in more temperate regions
7. Xenopsylla cheopis		X	X	X			X	X	Cosmopolitan
8. X. vexabilis		X	X				X	X	SE Asia (Thailand, Cambodia, Philippines), Australia, New Guinea, New Zealand, Kermadec Is.
Rhopalopsyllidae									
9. Parapsyllus laysanensis Wilson, n. sp.	X								
Ceratophyllidae									
10. Nosopsyllus fasciatus			X				X	X	Cosmopolitan
Leptopsyllidae									
11. Leptopsylla segnis		X	X				X	X	Cosmopolitan

[1] *Unlisted islands and islets lack positive records.*

Table 2. Host Associations of Hawaiian Siphonaptera

Siphonaptera \ Host	Branta sandvicensis	Diomedea immutabilis nest	Gallus gallus	Lophortyx californicus	Passer domesticus	P. domesticus nest	Puffinus pacificus nest	In & about poultry buildings	Bos taurus	Canis familiaris	C. familiaris shed	Felis catus	Herpestes auropunctatus	H. auropunctatus den	Homo sapiens	Mus musculus	M. musculus nest	Oryctolagus cuniculus	Rattus exulans	R. exulans nest	R. norvegicus	R. norvegicus nest	R. rattus	R. rattus nest	Sus scrofa	Beaches	In & about houses
Pulicidae																											
1. Echidnophaga gallinacea	X		X	X	X	X		X		X		X	X			X		X	X		X		X		X		?
2. Pulex irritans										X	X		?						?		?		?		X		X
3. P. simulans										X																	X
4. Pulex sp.										X	X		X		X												
5. Ctenocephalides felis felis									X	X		X	X	X	X	X		X	X	X	X		X			X	X
6. C. canis										X	X	?			?	?			?		?		?				?
7. Xenopsylla cheopis										X			X		X	X	X	X	X	X	X	X	X				X
8. X. vexabilis													X		X	X	X		X	X	X	X	X	X			X
Rhopalopsyllidae																											
9. Parapsyllus laysanensis Wilson, n. sp.		X					X																				
Ceratophyllidae																											
10. Nosopsyllus fasciatus													X			X			X	X	X	X	X				
Leptopsyllidae																											
11. Leptopsylla segnis													X			X	X		X	X	X	X	X				

SYSTEMATICS

KEY TO THE SPECIES OF FLEAS OF THE HAWAIIAN ISLANDS

1. Eye well developed 2
   Eye reduced . . . . . 11. *Leptopsylla segnis* (p. 35)

2. Genal comb (gen.cb.) present (*Ctenocephalides*) 3
   Genal comb absent or represented by single inconspicuous tooth . . 4

3. First spine of genal comb about half as long as second; head relatively short and rounded . . . . . 6. *Ctenocephalides canis* (p. 19)
   First spine of genal comb not much shorter than second; head elongated and sloping . . . . . 5. *Ctenocephalides felis felis* (p. 15)

4. Pronotal comb (pr.cb.) present . . . . . 10. *Nosopsyllus fasciatus* (p. 33)
   Pronotal comb absent 5

5. Frons evenly rounded 6
   Frons angulate . . . . . 1. *Echidnophaga gallinacea* (p. 10)

6. Pleural rod (pl.r.) present 7
   Pleural rod absent (*Pulex*) 9

7. Frontal tubercle (fr.tub.) present, arrowhead-shaped . . . . . 9. *Parapsyllus laysanensis* Wilson, n. sp. (p. 31)
   Frontal tubercle absent (*Xenopsylla*) 8

8. Distal arm of sternum IX (d.a.st.IX) curved upward at apex, ventrocaudal margin darkly pigmented; ventral margin of hilla (hi.) extended well below ventral margin of bulga (bu.) . . . . . 8. *Xenopsylla vexabilis* (p. 23)
   Distal arm of sternum IX not appreciably curved upward at apex, lightly pigmented throughout; ventral margin of hilla and bulga almost on one plane . . . . . 7. *Xenopsylla cheopis* (p. 20)

9. Crochet (cr.) rod-shaped (females not separable) . . 3. *Pulex simulans* (p. 14)
   Crochet triangular . . . . . 2. *Pulex irritans* (p. 12)

PULICIDAE

1. *ECHIDNOPHAGA GALLINACEA* (WESTWOOD)

(Figures 2-4)

Sarcopsyllus gallinaceus Westwood, 1875, Ent. Mon. Mag. 11:246.
Xestopsylla gallinacea: Illingworth, 1915, Haw. Forester Agr. 12:130.--Illingworth, 1915, Proc. Haw. Ent. Soc. 3:113.
Echidnophaga gallinacea: Illingworth, 1915, J. Econ. Ent. 8:492.--Illingworth, 1916, Proc. Haw. Ent. Soc. 3:252.--Timberlake et al., 1921, Proc. Haw. Ent. Soc. 4:609.--Illingworth, 1923, Proc. Haw. Ent. Soc. 5:270.--Ewing, 1924, Proc. Ent. Soc. Wash. 26:210.--Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44.--Bice, 1932, Haw. Agr. Exp. Sta. Circ. 5:36.--Eskey, 1934, Pub. Hlth. Bull. No. 213:13-18, 33, 48-50, 60.--Shaftesbury, 1934, J. Elisha Mitchell Sci. Soc. 49:248.--Anonymous, 1935, Pub. Hlth. Rep. 50:256.--Stiles & Baker, 1935, Nat. Inst. Hlth. Bull. No. 163:1090.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Alicata, 1942, J. Wash. Acad. Sci. 32:57.--Ewing & Fox, 1943, U.S. Dept. Agr. Misc. Pub. No. 500:121.--Pemberton, 1943, Haw. Med. J. 2:192.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 290.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Rumreich & Koepke, 1945, Pub. Hlth. Rep. 60:1422.--Alicata, 1947, Pacif. Sci. 1:71, 77, 78, 80, 81.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:28-30, 32, 35, 36, 38-40.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:227.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Hopkins & Rothschild, 1953, An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History), vol. I, p. 94.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50.--Fullaway, 1959, Proc. Haw. Ent. Soc. 17:23.--Becklund, 1964, Am. J. Vet. Res. 25:1399, 1405, 1412.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 43, 46, 70, 74, 78, 85, 86, 96, 100, 101, 107, 108, 111, 114.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Feb. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 20, 31.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Dec. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 10, 16.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., pp. 274, 281.--Muirhead-Thomson, 1968, Ecology of Insect Vector Populations, pp. 107, 108.--Tomich et al., 1968, Pacif. Sci. 22:363.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 200.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 55, 59, 86, 90, 95, 109-110, 134, 139, 141, 150, 151, 155, 159.--Kramer, 1971, Hawaiian Land Mammals, pp. 133, 148.
Sarcopsylla gallinacea: Wilcox, 1915, Rep. Haw. Agr. Exp. Sta. 1914, p. 24.--Fullaway, 1922, Proc. Haw. Ent. Soc. 5:12.
Echidnophaga gallinacea gallinacea: Costa Lima & Hathaway, 1946, Monogr. Inst. Oswaldo Cruz No. 4:135, 136.
Echidnophaga gallinaceae (sic)*:* Schwartz & Schwartz, 1949, A Reconnaissance of the Game Birds in Hawaii, p. 167.--Schwartz & Schwartz, 1950, Auk 67:25.

DISTRIBUTION. Widespread in tropical and subtropical areas; occasional in some cooler regions.

KAUAI. Haena, 2 m: 4 ♀♀, ex *Canis familiaris*, Mar. 1964, N. Wilson. Hanapepe: 1 ♂, 9 ♀♀, ex 3 *C. familiaris*, Mar. 1964, NW & G. E. Haas. Waimea Dist.: 13 ♂♂, 19 ♀♀, ex 60 *Rattus norvegicus*, June 1960, J. T. Kajiwara; 2 ♂♂, 4 ♀♀, ex 11 *Rattus exulans*, Dec. 1960, JTK.

OAHU. Recorded by Illingworth (1915b) from chickens and poultry yard and (1915a,c) from chickens, chicken roosting boards, chicken houses, and English sparrows; recorded by Wilcox (1915) from chickens, chicken yards, chicken bldgs., rats, and cats in Honolulu; recorded by Illingworth (1916) from chickens, chicken roosting board, and hen house; recorded by Bridwell (1917) from sparrow nests in a cavelike excavation at the side of Diamond Head road; recorded by Illingworth (1923) from poultry; recorded by Eskey (1934) from rats in Aiea, Honolulu, Kipapa, Waimanalo, and Waipahu; recorded by Alicata (1942) from a dog in Honolulu; recorded by Rumreich and Koepke (1945) from commensal rats in Honolulu; recorded by Cole and Koepke (1947b) from mongooses, *Rattus hawaiiensis, R. norvegicus*, and *Rattus rattus* in Honolulu;

recorded by Hopkins and Rothschild (1953). *ADDITIONAL RECORDS*. Honolulu (Fort Armstrong): 1 ♀, ex *Felis catus*, June 1947, C. R. Joyce; (Kaimuki): 22 ♀♀, ex *R. norvegicus*, Jan. 1939, C. E. Pemberton; (Manoa Valley): 1 ♂, 2 ♀♀, ex *R. rattus*, Dec. 1941, CEP; (Quarantine Station): 8 ♀♀, ex *C. familiaris*, May 1964. Kailua: 1 ♂, 2 ♀♀, ex *F. catus*, Apr. 1928. Koko Head: 1 ♀, ex *C. familiaris*, "fall" 1967, P. W. Schaefer.

MANANA (1.3 km off SE tip of Oahu). Recorded by Tomich et al. (1968) from *Oryctolagus cuniculus.*

MOLOKAI. Kaunakakai, 3 m: 3 ♂♂, ex *C. familiaris*, Feb. 1965, GEH & P. Q. Tomich.

MAUI. Recorded by Eskey (1934) from rats in Haiku, Kahului, Kailua, Kula, Lower Paia, Makawao, Olinda, Puunene, Upper Paia (Paia), and Wailuku; recorded by Hopkins and Rothschild (1953) from rats. *ADDITIONAL RECORDS*. Haleakala Crater (Kapalaoa cabin), 2,217 m: 3 ♂♂, 3 ♀♀, ex *Herpestes auropunctatus*, Feb. 1964, D. M. Tsuda. Keokea (Kula area): 1 ♀, ex *H. auropunctatus*, Dec. 1966, W. Garcia. Kihei: 8 ♂♂, 25 ♀♀, ex 5 *H. auropunctatus*, Oct. 1966, WG; 2 ♂♂, 6 ♀♀, ex 23 *R. rattus*, Nov. 1966, WG. Lahaina: 8 ♂♂, 18 ♀♀, ex 27 *H. auropunctatus*, Dec. 1966, WG. Omaopio area (Makawao Dist.): 1 ♂, 3 ♀♀, ex 8 *H. auropunctatus*, Sept., Oct. 1966, WG.

HAWAII. Recorded by Fullaway (1922) in Waimea (Kamuela); recorded by Ewing (1924) from *Herpestes birmanicus* and *C. familiaris* in Honokaa; recorded by Pemberton (1925) from cats and dogs in the Hamakua Dist.; recorded by Eskey (1934) from rats in Hilo, Honokaa, Kalopa, Kukaiau, Kukuihaele, Lower Pohakea, Olaa (Keaau), and the S Hilo Dist.; recorded by Gross and Bonnet (1951) in the Hamakua Dist.; recorded by Hopkins and Rothschild (1953) from rats in Honokaa; recorded by Kartman and Lonergan (1955) in the Hamakua Dist.; recorded by Fullaway (1959) from a nene goose at Pohakuloa; recorded by Malley and Devick (1968) from mongooses and rodents. *ADDITIONAL RECORDS*. Halaula (Kohala Mill), 64 m: 2 ♂♂, 1 ♀, ex *C. familiaris*, May 1964, G. P. Mills & T. Sagucio. Humuula, 2,043 m: 1 ♂, 12 ♀♀ ; 10 ♂♂, 18 ♀♀, ex *H. auropunctatus*, May 1969, PQT. Kawaihae, 15 m: 2 ♂♂, 7 ♀♀, ex *C. familiaris*, May 1964, GPM & TS. Kukaiau Ranch (NE slope Mauna Kea), 1,952 m: 1 ♂, 11 ♀♀, ex *H. auropunctatus*, Feb. 1964, GPM & TS. Makahalau Camp, 1,171 m: many, ex *C. familiaris* & *H. auropunctatus*, Nov. 1962, GEH & GPM. Napoopoo: 1 ♂, 16 ♀♀, ex *C. familiaris*, Jan. 1962, NW; (1.4 km N: Hikiau Heiau), 5 m: 2 ♀♀; 6 ♀♀, ex 1, 3 *H. auropunctatus*, Jan., Feb. 1962, NW & S. Kaaekuahiwi. Niulii, 46 m: 3 ♂♂, 7 ♀♀, ex 2 *C. familiaris*, May 1964, GPM & TS. Onomea, 76 m: 5 ♀♀, ex *C. familiaris*, May 1964, GPM & TS. Puako (beach park), 3 m: 2 ♂♂, 15 ♀♀, ex 3 *H. auropunctatus*, July 1968, SK & E. Auna. Puu Kihe (NE slope Mauna Kea, cabins), 2,364 m: 3 ♀♀, ex *H. auropunctatus*, July 1968, SK & EA. Umikoa (Kukaiau Ranch Headquarters), 1,067 m: 3 ♀♀, ex *H. auropunctatus*, Feb. 1964, GPM & TS. Waikii (5.2 km SSE: Kilohana Girl Scout Camp), 1,708 m: 10 ♀♀, ex *H. auropunctatus*, July 1962, W. Graf.

HOSTS. Recorded from *Branta sandvicensis, Gallus gallus* and roosts, yards, and houses, *Lophortyx californicus, Passer domesticus* and nest, *C. familiaris, F. catus, H. auropunctatus, Mus musculus, O. cuniculus, R. exulans, R. norvegicus, R. rattus*, and *Sus scrofa*.

The sticktight flea, *E. gallinacea*, was first recorded from Hawaii by Illingworth (1915a). The approximate date of introduction of *E. gallinacea* is the best documented of all fleas. Its sudden and noticeable appearance on chickens in Honolulu resulted in a series of papers: Illingworth (1915a,b,c, 1916) and Wilcox (1915). Illingworth (1915a) reported that entomologists had not noticed this flea prior to 1913 and that the first specimens in the College of Hawaii collection were taken in November 1913. In his report for 1914, Wilcox (1915) reported this flea's appearance in Honolulu during the past year (1913). To determine the date of introduction and the rate of spread between and on the islands, Illingworth (1915a) asked poultry owners and others to submit a postcard stating when and where the fleas were first noticed. We have found neither published nor unpublished results of this survey. We know, however, from Fullaway (1922) that by May 1921 *E. gallinacea* had spread to the Island of Hawaii. It was not recorded from Maui until Eskey's (1934) report. Our Kauai and Molokai records appear to be the first ones for

those islands. The presence of sticktight fleas on Lanai is probable.

We concur with Illingworth (1915a) that the source of *E. gallinacea* was quite probably poultry from California. As this flea also parasitizes mammals, such as dogs, cats, and rats, poultry may not have been the sole means of transport between Oahu and the other islands.

E. gallinacea is widely distributed altitudinally between sea level and 2,364 m (Puu Kihe Cabins, Mauna Kea). It occurs in the arid zone around Kawaihae Bay (average annual rainfall less than 188 mm) to wet Onomea (rainfall about 3,476 mm). Apparently elevation (temperature) is not a limiting factor, but extremely heavy rainfall may be detrimental. Although it occurs on five of the main islands, *E. gallinacea* is seemingly absent from many localities, and where found it has typically a distribution referred to as "contagious" by Cole and Koepke (1947b). Most specimens aggregate onto one or a few of several seemingly equally suitable host animals. The sessile females frequently clump together to form a crustlike group.

A peculiarity in the geographic distribution of *E. gallinacea* on the Island of Hawaii is the continued absence of this flea from rats and other mammals in the enzootic plague area following the general application of DDT around dwellings between 1945 and 1961. From 1932 (Eskey, 1934) to February 1954, plague surveillance personnel found sticktight fleas on rats trapped in the area.

The seasonal occurrence of the sticktight flea, based primarily on data from *R. norvegicus*, had a peak during July-October and a low during April-June (Eskey, 1934). Our data indicate that the sex ratio of individuals on hosts is unequal in favor of females.

E. gallinacea has the widest host range of the fleas occurring in the islands. Birds generally are considered true hosts, but many mammals are well-known hosts, and some, such as dogs and mongooses, probably qualify as true hosts in Hawaii.

Eskey (1934) reported that adult male rats were more frequently infested than females and that young rats were rarely infested. He pooled species of rats in each locality so it is impossible to know if all three species were infested in all localities. Of the three species of rats, *R. norvegicus* had the heaviest infestation (Eskey, 1934, Cole and Koepke, 1947b). Eskey (1934) was first to record *M. musculus* as a host, but he did not specify on which island(s) the infested mice (and mongooses) were trapped. Other original host records not located on any particular island are pigs by Bonnet (1948) and California quail by Schwartz and Schwartz (1949).

2. *PULEX IRRITANS* LINNAEUS

(Figures 5-9)

Pulex irritans Linnaeus, 1758, Syst. Nat., 10th ed., I:614.

Pulex irritans: Bryan, 1915, Natural History of Hawaii, p. 401.--Eskey, 1934, Pub. Hlth. Bull. No. 213:13, 50.--Anonymous, 1935, Pub. Hlth. Rep. 50:257.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Pemberton, 1943, Haw. Med. J. 2:191.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 289.--Fullaway & Krauss, 1945, Common Insects of Hawaii, p. 24, pl. I, fig. 30.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:227.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50.--Nichols, 1963, State Haw., Div. Fish Game, Hnl., Proj. W-5-R-14, p. 7.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 86, 101, 107, 113, 114.--Haas & Wilson, 1967, J. Med. Ent. 4:25-29.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Feb. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 11, 41.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Dec. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 6, 21.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., pp. 278, 281.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p.

201.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 55, 90, 110, 141, 142, 150, 157, 159.--Tomich, 1969, Mammals in Hawaii: a synopsis and notational bibliography, p. 178.--Haas et al., 1971, Haw. J. Hist. 5:60, 70.--Kramer, 1971, Hawaiian Land Mammals, pp. 133, 203.

Pulex irritans [partim]: Ewing, 1924, Proc. Ent. Soc. Wash. 26:209.--Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44.

DISTRIBUTION. Cosmopolitan.

OAHU. Recorded by Eskey (1934) from premises of householders in Honolulu and from rats.

MAUI. Recorded by Eskey (1934) from rats.

HAWAII. Recorded by Ewing (1924) from *Canis familiaris* in Honokaa; recorded by Pemberton (1925) from dogs in the Hamakua Dist.; recorded by Eskey (1934) from dogs and rats in the Hamakua Dist. and from rats in the Hilo and vicinity sector; recorded by Gross and Bonnet (1951) in the Hamakua Dist.; recorded by Kartman and Lonergan (1955) in the Hamakua Dist.; recorded by Haas and Wilson (1967) from *C. familiaris* in Haina, Hilo, Honokaa, Humuula, Kahua Ranch, Kapulena, Kukuihaele, Ookala, Paauilo, Pohakuloa, Puuanahulu, Puu Waawaa Ranch, and Umikoa, and from *Sus scrofa* in Hanaipoe; recorded by Malley and Devick (1968) from dogs. *ADDITIONAL RECORDS.* Humuula, 2,043 m: 8 ♂♂, 19 ♀♀, in abandoned dog shed, Aug. 1968, S. Kaaekuahiwi & E. Auna; 4 ♂♂, 5 ♀♀, in abandoned dog shed, Mar. 1969, P. Q. Tomich; 3 ♂♂, 5 ♀♀, ex *C. familiaris*, Mar. 1969, PQT; 3 ♂♂, ex *C. familiaris* (from Kamuela), Mar. 1969, PQT; 3 ♂♂, 4 ♀♀; 1 ♂, 4 ♀♀; 1 ♂, 7 ♀♀; 1 ♂, ex *C. familiaris* (4th host from Kamuela), Apr. 1969, PQT; 2 ♂♂, ex *C. familiaris*, Aug. 1969, PQT. Puu Laau (1.6 km NE: Kamakoa Gulch), 2,700 m: 4 ♂♂, 4 ♀♀, ex *S. scrofa*, Nov. 1969, J. G. Giffin; (0.8 km NE), 2,300 m: 2 ♂♂, 2 ♀♀, ex *S. scrofa*, Mar. 1970, JGG.

HOSTS. Recorded from *C. familiaris, Herpestes auropunctatus*, rats, *S. scrofa*, an abandoned dog shed, and premises of householders (?houses and yards).

The human flea, *P. irritans*, was first recorded by Bryan (1915), but his statement is presumptive rather than based on specimens examined critically. Any records that cannot be verified by examination of specimens must be placed in doubt because in most localities the probability is greater that the species is *Pulex simulans*. This is especially true for specimens collected near sea level. An added difficulty is that only males have morphologically distinguishing characters.

P. irritans perhaps was introduced originally on dogs in the eighteenth or nineteenth century. The earliest confirmed collection of *P. irritans* is by Pemberton on 17 December 1922 (see Haas and Wilson, 1967). He collected a male from a dog in Honokaa. At the same time and place he also collected at least two males of *P. simulans*. Ewing (1924) recorded all 14 of Pemberton's specimens (sex not specified) as *P. irritans*. Eskey (1934) again recorded human fleas from the Island of Hawaii and added Oahu and Maui. He was first to record *P. irritans* on rats and a mongoose, but he did not specify on which island the infested mongoose was trapped.

We are unable to confirm the occurrence of *P. irritans* on any island other than Hawaii (Table 1), and there it was found only to the north and rarely in areas near sea level. It occurred in the mountains as high as 2,043 m at Humuula. The altitudinal distribution of *P. irritans* is the type expected of a flea adapted to a temperate rather than subtropical climate.

As related to average annual rainfall, *P. irritans* does not range down into the low, hot semidesert around Kawaihae Bay (rainfall less than 188 mm); but it occurs with *P. simulans* in the high, cool, dry area at Pohakuloa (rainfall between 381 and 508 mm). The Kawaihae Bay area is undoubtedly too hot, so aridity cannot be considered as the limiting factor. The wettest locality that evidently has a resident population of *P. irritans* is Ookala (rainfall 2,921 mm). Thus in contrast to *P. simulans*, it has a much narrower geographic range.

Seasonal occurrence and sex ratio of *P. irritans* is unknown for lack of sufficient data. Only a few *P. irritans* females were captured alive and isolated for specific determination by rearing their male progeny.

The dog is a true host of *P. irritans*, and recent data suggest that the wild pig is at least a secondary host. Whether or not man should be classified as a true, secondary, or only accidental host is undecided for lack of sufficient data. We disagree with Pemberton (1943) that the cat is a normal host. He (Pemberton, 1925) recorded collecting 636 specimens of *P. irritans* from dogs, but none from cats. The cats had only cat fleas and sticktight fleas. The flea collection at the Hawaiian Sugar Planters' Association in Honolulu contains numerous fleas collected by Pemberton, but there is not one human flea from a cat. Therefore, his 1943 statement appears to be in error or is a generality not based on collections in Hawaii. Consequently, we do not accept subsequent statements based on Pemberton (1943) that *P. irritans* was found on cats in Hawaii. Furthermore, without specimens to reexamine, we must question Eskey's (1934) records of *P. irritans* from premises of householders, from rats, and a mongoose (Table 2).

3. *PULEX SIMULANS* BAKER

(Figure 10)

Pulex simulans Baker, 1895, Can. Ent. 27:65, 67.
Pulex irritans [partim]: Ewing, 1924, Proc. Ent. Soc. Wash. 26:209.--Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44.
?*Pulex irritans [partim]:* Eskey, 1934, Pub. Hlth. Bull. No. 213:13, 50.
Pulex simulans: Haas & Wilson, 1967, J. Med. Ent. 4:25-28.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., pp. 278, 281.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 202.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 90, 142.--Tomich, 1969, Mammals in Hawaii: a synopsis and notational bibliography, p. 178.--Haas et al., 1971, Haw. J. Hist. 5:60.

DISTRIBUTION. Nearctic and Neotropical Regions; Hawaiian Islands.
KAUAI. Recorded by Haas and Wilson (1967) from *Canis familiaris* in Haena.
OAHU. Recorded by Haas and Wilson (1967) from under a house in Honolulu.
HAWAII. Recorded by Haas and Wilson (1967) from *C. familiaris* in Captain Cook, Glenwood, Haina, Hakalau, Halaula School (grounds), Halawa, Hawi, Hilo, Holualoa, Honalo, Honaunau, Honohina, Honokaa, Honokahau, Honomu, Hookena, Humuula, Kahaluu, Kailua, Kaimu, Kainaliu, Kalapana, Kamuela, Kapaau, Kapoho, Kapulena, Kaumana, Kawaihae, Kealakekua, Kealia, Keauhou, Keauhou Ranch, Keaukaha, Kilauea Military Camp, Kohala Mill, Kukaiau, Kukuihaele, Kupaahu, Kurtistown, Laupahoehoe, Mahukona, Makahalau, Makapala, Milolii, Mountain View, Naalehu, Napoopoo, Ninole, Niulii, Olaa, Onomea, Ookala, Paauhau, Paauilo, Pahala, Pahoa, Papaaloa, Papaikou, Pepeekeo, Piihonua, Pohakea Ranch, Pohakuloa, Pohoiki, Puako, Punaluu, Puu Waawaa (Ranch), Puuanahulu, Umikoa, Waiakea Camp No. 6, Waikii, Waiohinu, Waipio Valley, and Wood Valley; recorded by Malley and Devick (1968) from dogs. *ADDITIONAL RECORDS*. Honokaa: 2 ♂♂, ex *C. familiaris*, Dec. 1922, C. E. Pemberton. Humuula, 2,043 m: 1 ♂, ex *C. familiaris* (from Kamuela) Mar. 1969, P. Q. Tomich; 4 ♂♂, ex *C. familiaris* (from Kamuela), Apr. 1969, PQT; 1 ♂, ex *C. familiaris*, Aug. 1969, PQT. Waipio Valley, 5 m: 1 ♂, 1 ♀, under house, Nov. 1969, PQT.

HOSTS. Recorded from *C. familiaris* and under house.

P. simulans was not discovered in Hawaii until Wilson collected a specimen in December 1963 at Punaluu, Hawaii (see Haas and Wilson, 1967). Earlier investigators misdetermined specimens as *Pulex irritans*, and the time of original introduction may have been many years before Pemberton's confirmed collection of

17 December 1922 (see Haas and Wilson, 1967). Dogs brought from North, Central, or South America were probably the agents by which *P. simulans* gained entrance into the islands.

P. simulans is much more widespread than *P. irritans*. There are no apparent limitations imposed by elevation or rainfall. *P. simulans* ranges from near sea level up to Humuula at 2,043 m and from around Kawaihae Bay with its very low rainfall of less than 188 mm to Piihonua with an average annual rainfall of 6,362 mm (see Haas and Wilson, 1967). Seasonal occurrence of *P. simulans* is unknown for lack of adequate data. Sex ratio is unknown, but males are probably outnumbered by females.

Haas and Wilson (1967) redetermined as *P. simulans*, two males that Pemberton collected on 17 December 1922 and Ewing (1924) recorded as *P. irritans*. Recently two more males of *P. simulans* from this same lot were found in the Hawaiian Sugar Planters' Association insect collection.

P. irritans and *P. simulans* females cannot be reliably separated morphologically. Females unassociated with males are listed as *Pulex* sp. in the following section.

4. *PULEX* SP.

Pulex sp.: Haas & Wilson, 1967, J. Med. Ent. 4:30.

KAUAI. Recorded by Haas and Wilson (1967) from *Canis familiaris* in Kaumakani, Kokee, and Wailua.

HAWAII. Recorded by Haas and Wilson (1967) from *C. familiaris* in Haina, Hilo, Honaunau, Honokaa, Humuula, Kamuela, Kukuihaele, Mountain View, Napoopoo, Niulii, Onomea, Ookala, Paauhau, Paauilo, Pohakuloa, Puako, and Puuanahulu, and from *Homo sapiens* in Honokaa. *ADDITIONAL RECORDS*. Hawi, 180 m: 1 ♀, ex *Herpestes auropunctatus*, Aug. 1968, S. Kaaekuahiwi & E. Auna. Humuula, 2,043 m: 3 ♀♀, ex *C. familiaris* (from Kamuela), Mar. 1969, P. Q. Tomich; 9 ♀♀, ex *C. familiaris* (from Kamuela), Apr. 1969, PQT; 2 ♀♀, in dog shed soil, Apr. 1969, PQT; 10 ♀♀, ex *C. familiaris*, Aug. 1969, PQT. Parker Ranch (NW slope Mauna Kea, Kemole Gulch), 2,195 m: 2 ♀♀, ex *Sus scrofa*, Jan. 1971, J. G. Giffin.

HOSTS. Recorded from *C. familiaris, H. auropunctatus, H. sapiens, S. scrofa*, and dog shed.

5. *CTENOCEPHALIDES FELIS FELIS* (BOUCHÉ)

(Figures 11-14)

Pulex Felis Bouché, 1835, Nova Acta Leop.-Carol. 17:505.

Ctenocephalus felis: McCoy & Bowman, 1914, Pub. Hlth. Rep. 29:1634.--Ewing, 1924, Proc. Ent. Soc. Wash. 26:210.--Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44.--Pemberton, 1926, Proc. Haw. Ent. Soc. 6:221.--Swezey & Bryan, 1927, Proc. Haw. Ent. Soc. 6:422.--Eskey, 1934, Pub. Hlth. Bull. No. 213:13.--Pemberton, 1934, Proc. Haw. Ent. Soc. 8:509.

Ctenocephalides felis felis: Eskey, 1934, Pub. Hlth. Bull. No. 213:13, 14, 16-18, 33, 50.--Anonymous, 1935, Pub. Hlth. Rep. 50:257.--Hopkins & Rothschild, 1953, An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History), vol. I, p. 152.--Hopkins, 1961, Insects of Micronesia 14:96.--Haas, 1966, J. Med. Ent. 2:321.--Krampitz, 1968, Z. Tropenmed. Parasit. 19:302.--Tomich et al., 1968, Pacif. Sci. 22:362.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 199.--Haas et al., 1971, Haw. J. Hist. 5:60.

Ctenocephalides felis: Stiles & Baker, 1935, Nat. Inst. Hlth. Bull. No. 163:1090.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Pemberton, 1943, Haw. Med. J. 2:191.--Pemberton, 1945, Proc.

Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Rumreich & Koepke, 1945, Pub. Hlth. Rep. 60:1422.--Alicata, 1947, Pacif. Sci. 1:77, 78, 80.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:28-30, 32, 35, 36, 38-40.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:227.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50.--Ruhle, 1959, A Guide for the Haleakala Section Island of Maui, Hawaii,p. 86.--Becklund, 1964, Am. J. Vet. Res. 25:1405.--Mitchell, 1964, Proc. Haw. Ent. Soc. 18:414, 415.--Gubler, 1966, J. Med. Ent. 3:161.--Haas, 1966, J. Med. Ent. 2:321, 323, 324.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 46, 74, 78, 79, 85, 86, 96, 101, 107, 108, 114.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Feb. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 4, 30.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Dec. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 3, 15.--Hinton & Dunn, 1967, Mongooses, p. 108.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., p. 281.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 199.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 55, 59, 87, 90, 95, 96, 109, 110, 134, 141, 149, 150, 151, 159.--Tomich, 1969, Mammals in Hawaii: a synopsis and notational bibliography, p. 178.--Tomich, 1969, J. Wildl. Mgmt. 33:576.--Haas et al., 1971, Haw. J. Hist. 5:60.--Kramer, 1971, Hawaiian Land Mammals, pp. 133, 148.

DISTRIBUTION. Cosmopolitan.

KAUAI. Haena, 2 m: 1 ♂, 4 ♀♀, ex *Canis familiaris*, Mar. 1964, N. Wilson. Hanapepe: 12 ♂♂, 14 ♀♀, ex *C. familiaris*, Mar. 1964, NW & G. E. Haas. Kalaheo: 4 ♀♀, ex *C. familiaris*, Apr. 1964, Mrs. Yamase; 1 ♀, ex *C. familiaris*, Apr. 1964, S. Inouye; 2 ♀♀, ex *C. familiaris*, Dec. 1964, SI; 1 ♂, 1 ♀, ex *C. familiaris*, Dec. 1964, E. Au. Kilauea: 1 ♂, ex *C. familiaris*, Mar. 1964, NW. Kipu: 4 ♂♂, 5 ♀♀, ex *C. familiaris*, Apr. 1964, J. Hashimoto. Kokee (?State Park): 1 ♀, Aug. 1921, O. H. Swezey. Koloa: 6 ♀♀, ex *C. familiaris*, Apr. 1964, Shigematsu. Lawai: 4 ♂♂, 6 ♀♀, ex *C. familiaris*, May 1964, S. Au; 3 ♀♀, ex *C. familiaris*, Apr. 1964, N. Horita. Lihue: 13 ♀♀, ex *Felis catus*, May 1964, SA. Makaweli, 2 ♀♀, ex *C. familiaris*, Apr. 1964, S. Itakura. Omao: 8 ♀♀, ex *C. familiaris*, Apr. 1964, W. Kageyama. Puhi: 4 ♂♂, 5 ♀♀, ex *C. familiaris*, Apr. 1964, T. Caneles. Wailua: 9 ♂♂, 3 ♀♀, ex *F. catus*, Apr. 1964, SA; 1 ♂, 3 ♀♀, ex *C. familiaris*, Apr. 1964, K. Yama. Waimea Dist.: 1 ♂, ex *Rattus norvegicus*, June 1960, J. T. Kajiwara.

OAHU. Probably recorded (as *C. canis*) by Van Dine (1908) in residences in Honolulu; recorded by Eskey (1934) from rats in Aiea, Honolulu, Kipapa, Waimanalo, and Waipahu; recorded by Pemberton (1934) from houses and yards in Honolulu; recorded (Eskey, 1934) by Anonymous (1935) from rats in Honolulu; recorded by Rumreich and Koepke (1945) from commensal rats in Honolulu; recorded by Cole and Koepke (1947b) from mongooses, *R. norvegicus*, and *Rattus rattus* in Honolulu; recorded by Hopkins and Rothschild (1953) from a mongoose in Honolulu; recorded by Mitchell (1964) from *Rattus exulans* in Manoa Valley. *ADDITIONAL RECORDS*. Ewa Beach (Keahi Point): 1 ♀, ex *F. catus*, May 1966. Hickam Air Force Base: 4 ♂♂, 14 ♀♀, 5 larvae, 1 egg, ex *C. familiaris*, Feb. 1967, R. H. McMasters. Honolulu: 1 ♀, Apr. 1922, Q. C. Chock; 3 ♂♂, 7 ♀♀, ex *F. catus*, Mar. 1934, E. H. Bryan, Jr.; 2 ♀♀, ex *Bos taurus*, Oct. 1945, E. H. Willers; 14 ♂♂, 28 ♀♀, in house, Feb. 1960, S. Quate; 25 ♂♂, 41 ♀♀, ex *C. familiaris*, Nov. 1960, S & L. W. Quate; 2 ♂♂, 8 ♀♀, ex *C. familiaris*, Mar. 1962, C. J. Lathrop; 1 ♀, ex *Herpestes auropunctatus*, Nov. 1963, D. M. Tsuda; 1 ♂, ex *Homo sapiens*, Feb. 1964, DMT; 1 ♀; 2 ♂♂, 3 ♀♀, ex *H. sapiens*, May 1964, DMT; 1 ♂, 5 ♀♀, ex *F. catus*, May 1964, H. Arakaki; 2 ♂♂, 6 ♀♀, ex *H. auropunctatus*, June 1964, W. J. Voss; 1 ♀, ex *F. catus*, Aug. 1964, J. C. Harrell; 11 ♀♀, ex *F. catus*, Dec. 1964, EA; 2 ♂♂, 3 ♀♀, ex *F. catus*, Jan. 1965, HA; 4 ♂♂, 9 ♀♀, in dwelling, Mar. 1965, DMT; 3 ♂♂, 5 ♀♀, ex *F. catus*, May 1965, JCH; 2 ♀♀, 1 larva, ex *C. familiaris*, Jan. 1967, HA; 1 ♀, ex *F. catus*, Mar. 1967, E. E. Gless; (Ala Moana Park): 1 ♀, ex *H. sapiens*, Nov. 1964, WJV; (Bishop Museum grounds): 2 ♂♂, 4 ♀♀, ex *C. familiaris*, Apr. 1965, WJV; (Diamond Head Beach Park): 1 ♂, 7 ♀♀, Nov. 1914; (Manoa Valley): 2 ♂♂, 1 ♀, ex *R. rattus*, Dec. 1941, C. E. Pemberton; 1 ♂, 6 ♀♀, under house, Feb. 1946, R. H. Van Zwaluwenburg. Kailua: 1 ♀, ex *F. catus*, Apr. 1928; larvae, eggs, ex *F. catus*, June 1959, D. Rainwater. Kaneohe: 1 ♂, ex *H. auropunctatus*, May 1948, C. R. Joyce. Kaneohe Marine Corps Air Station (Mokapu Point): 1 ♂, ex *H. auropunctatus*, Jan. 1967, J. H. Fitch & D. I. Hoff. Koko Head: 4 ♀♀, ex *C. familiaris*, "fall" 1967, P. W. Schaefer. Red Hill Navy Reservation: 1 ♂, 5 ♀♀, ex *H. auropunctatus*, July 1967, DMT. Tantalus: 3 ♂♂, 7 ♀♀, under houses, Apr., May 1940, CEP; 5 ♀♀, ex 2 *H. auropunctatus*, July, Aug. 1963, DMT.

MANANA (1.3 km off SE tip Oahu). Recorded by Tomich et al. (1968) from *Oryctolagus cuniculus*. *ADDITIONAL RECORD*. 4 ♂♂, 7 ♀♀, ex *O. cuniculus*, Aug. 1968, D. L. Burckhalter.

MOLOKAI. Recorded by Swezey and Bryan (1927) from a rat at McVeigh's cabin, near rim of Waikolu Valley at 3,370 feet (1,028 m). *ADDITIONAL RECORDS*. Honomuni (E. Molokai): 1 ♂, 3 ♀♀, ex *C. familiaris*, Nov. 1964, N. Pekelo, Jr. Hoolehua: 6 ♀♀, ex *C. familiaris*, Nov. 1964, NP. Kaunakakai: 5 ♀♀, ex *C. familiaris*, Nov. 1964, NP; many, ex 6 *C. familiaris*, Feb. 1965, GEH & P. Q. Tomich. Maunaloa: 3 ♂♂, 4 ♀♀, ex *C. familiaris*, Nov. 1964, NP.

LANAI. Lanai City, 534 m: 1 ♀, ex *C. familiaris*, May 1962, GEH; 5 ♀♀, ex *Rattus* sp., Apr. 1964, D. Willett; 7 ♂♂, 14 ♀♀, ex *C. familiaris*, Apr. 1964, DW.

MAUI. Recorded by Eskey (1934) from rats in Haiku, Kailua, Kula, Lower Paia, Makawao, Olinda, Puunene, Upper Paia (Paia), and Wailuku; recorded (Eskey, 1934) by Anonymous (1935) from rats in central Maui; recorded by Hopkins and Rothschild (1953) from rats. *ADDITIONAL RECORDS*. Haiku: 1 ♂, 2 ♀♀, ex 3 *H. auropunctatus*, Mar. 1967, W. Garcia. Haleakala Crater (Kapalaoa cabin), 2,217 m: 2 ♀♀, ex *H. auropunctatus*, Feb. 1964, DMT. Kaheka area: 1 ♀, ex *H. auropunctatus*, Mar. 1967, WG. Keokea: 2 ♂♂, 3 ♀♀, ex 2 *H. auropunctatus*, Feb. 1967, WG; (Kula area): 1 ♀, ex *H. auropunctatus*, Dec. 1966, WG. Kihei, 3 m:1♂, 4♀♀, ex *F. catus*, Jan. 1965, WG; 2♂♂, 7♀♀, ex 5 *H. auropunctatus*, Oct. 1966, WG. Lahaina area: 19 ♂♂, 44 ♀♀, ex 27 *H. auropunctatus*, Dec. 1966, WG. Makawao, 500 m: many, ex *C. familiaris*, Jan. 1965, WG; 8 ♀♀, ex *F. catus*, Jan. 1965, WG; 5 ♂♂, 9 ♀♀, ex 8 *H. auropunctatus*, Aug. 1966, WG; 1 ♂, ex 30 *R. exulans*, Aug. 1966, WG. Olinda: 3 ♀♀, ex 3 *H. auropunctatus*, Mar. 1967, WG. Omaopio area, (Makawao Dist.): 3 ♂♂, 8 ♀♀, ex 8 *H. auropunctatus*, Sept., Oct. 1966, WG. Waiakoa, 915 m: 1 ♂, 1 ♀, ex *C. familiaris*, Feb. 1964, DMT. Wailuku, 101 m: many, ex *F. catus*, Jan. 1965, WG.

HAWAII. Recorded by McCoy and Bowman (1914) from rodents along the Hamakua Coast; recorded by Ewing (1924) from *C. familiaris* and *Herpestes birmanicus* in Honokaa and from *Felis domestica* in Waipio (?Valley) at 3,800 feet (1,159 m); recorded by Pemberton (1925) from cats and dogs in the Hamakua Dist.; recorded by Eskey (1934) from rats in Ahualoa, Hilo, Honokaa, Kalopa, Kukaiau, Kukuihaele, Laupahoehoe, Lower Pohakea, Olaa (Keaau), the S Hilo Dist., and Upper Pohakea; recorded (Eskey, 1934) by Anonymous (1935) from rats in Hilo and the Hamakua Dist.; recorded by Gross and Bonnet (1951) in the Hamakua region; recorded by Hopkins and Rothschild (1953) from rats in Honokaa; recorded by Kartman and Lonergan (1955) from the Hamakua Dist.; recorded by Haas (1966a) from *H. auropunctatus* from Waipio Valley to Paauilo in the Hamakua Dist., from Hawi to Niulii in the N Kohala Dist., and from Honaunau to Napoopoo in the S Kona Dist., from a hollow tree (mongoose den) near Kukuihaele, from a cat near Honokaa, from a nest probably of *R. exulans* near Kamuela, and from dogs; recorded by Malley and Devick (1968) from cats, mongooses, and dogs. *ADDITIONAL RECORDS*. Halaula (Kohala Mill), 64 m: 1 ♂, ex *C. familiaris*, May 1964, G. P. Mills & T. Sagucio. Hawi, 180 m: 6 ♂♂, 5 ♀♀, ex *H. auropunctatus*, Aug. 1968, S. Kaaekuahiwi & E. Auna. Hilo (dog pound): 3 ♂♂, 12 ♀♀, ex *C. familiaris* (from Puna Dist.), Feb. 1964, GPM & TS. Honaunau, 335 m: 1 ♀, ex *C. familiaris*, May 1964, GPM & TS. Honokaa: 1 ♂, 1 ♀, ex *C. familiaris*, Feb. 1962, NW. Humuula, 2,043 m: 3 ♂♂, 13 ♀♀, ex *C. familiaris* (from Kamuela), Mar. 1969, PQT; 8 ♀♀, ex *C. familiaris*, Mar. 1969, PQT; 4 ♂♂, 7 ♀♀; 1 ♂, 7 ♀♀, ex *C. familiaris*, Apr. 1969, PQT; 7 ♂♂, 33 ♀♀, ex *C. familiaris* (from Kamuela), Apr. 1969, PQT; 1 ♂, 3 ♀♀; 4 ♀♀; 2 ♂♂,3 ♀♀, ex *H. auropunctatus*, May 1969, PQT; 3 ♀♀, ex *C. familiaris*, Aug. 1969, PQT. Kahaluu (beach park), 3 m: 1 ♀, ex *R. exulans*, Dec. 1961, GEH. Kaimu, 6 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Kapaau (Kohala P.O.), 146 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Kaumana, 335 m: 4 ♂♂, ex *C. familiaris*, May 1964, GPM & TS. Kawaihae (Spencer Park), 3 m: 1 ♀; 1 ♀; 1 ♀; ex *H. auropunctatus*, July, Aug. 1968, SK & EA. Keanakolu (hunters' cabin), 1,613 m: many, ex *H. auropunctatus*, July 1968, SK & EA; (Parker Ranch Station), 1,650 m: 1 ♂, 3 ♀♀, ex *H. auropunctatus*, July 1968, SK & EA. Kukaiau Ranch (stone corral), 1,586 m: 1 ♂, 1 ♀, ex *H. auropunctatus*, Feb. 1964, GPM & TS. Mahukona, 3 m: 1 ♂, ex *H. auropunctatus*, Aug. 1968, SK & EA. Makahalau Camp, 1,171 m: 11 ♂♂, 41 ♀♀, ex *C. familiaris*, Feb. 1964, GPM; many, ex *H. auropunctatus*, Nov. 1962, GEH & GPM; 6 ♀♀, ex 2 *R. rattus*, Nov. 1962, GEH & GPM. Mountain View, 457 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Napoopoo: 3 ♂♂, 7 ♀♀, ex *C. familiaris*, Jan. 1962, NW; 2 ♂♂, 4 ♀♀, ex *F. catus*, Jan. 1962, NW. Onomea, 76 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Ookala, 91 m: 15 ♂♂, 22 ♀♀, ex *C. familiaris*, Feb. 1964, GPM & TS; 1 ♂, ex *Rattus* sp., Nov. 1945, B. Brookman. Pahoa, 195 m: 2 ♂♂, 2 ♀♀, ex *C. familiaris*, May 1964, GPM & TS. Palihooukapapa, 1,269 m: 1 ♂, ex *R. norvegicus*, Nov. 1962, GEH & GPM. Papaikou, 62 m: 1 ♂; 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Puako (beach park), 3 m: 1 ♂, 7 ♀♀, ex 3 *H. auropunctatus*, July, Aug. 1968, SK & EA. Punaluu, 3 m: 1

♀, ex *C. familiaris*, Dec. 1963, NW. Puu Kihe (NE slope Mauna Kea, cabins), 2,364 m: 3 ♂♂, 4 ♀♀, ex *H. auropunctatus*, July 1968, SK & EA; (NE slope Mauna Kea, forestry plot), 2,379 m: 1 ♂, 3 ♀♀, ex *H. auropunctatus*, July 1968, SK & EA. Puu Mali (N slope Mauna Kea, cabin), 1,982 m: 1 ♀, ex *H. auropunctatus*, Feb. 1964, GPM & TS. Puuanahulu, 667 m: 1 ♀, ex *C. familiaris*, Apr. 1964, GPM & TS. Umikoa, 1,055 m: many, ex *H. auropunctatus*, Feb. 1964, GPM & TS; (Kukaiau Ranch Headquarters), 1,067 m: 5 ♂♂, 20 ♀♀, ex *C. familiaris*, Feb. 1964, GPM & TS; 8 ♀♀, ex *H. auropunctatus*, July 1968, SK & EA. Volcano (2.4 km NW Volcano House: Keauhou Ranch), 1,251 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Waiakeauka: 30 ♂♂, 43 ♀♀, ex *C. familiaris*, Feb. 1964, GPM & TS. Waikii, 1,449 m: 2 ♂♂, 7 ♀♀, ex *H. auropunctatus*, Apr. 1969, PQT; (5.2 km SSE: Kilohana Girl Scout Camp), 1,708 m: 1 ♀, ex *H. auropunctatus*, July 1962, W. Graf; 1 ♀, ex *R. rattus*, Sept., 1964, R. I. Baldwin. Waiohinu, 351 m: 1 ♂, ex *C. familiaris*, May 1964, GPM & TS. Waipio Valley, 5 m: 78 ♂♂, 167 ♀♀, under house, Oct. 1969, PQT.

HOSTS. Recorded from bodies of *B. taurus, C. familiaris, F. catus, H. auropunctatus, H. sapiens, Mus musculus, O. cuniculus, R. exulans, R. norvegicus*, and *R. rattus*; in and about houses, yards, and beaches, a mongoose den, and a nest probably of *R. exulans*.

The cat flea, *C. felis*, was first recorded by McCoy and Bowman (1914) through specimens collected from rodents along the Hamakua Coast, Island of Hawaii. As early as 1907, however, Van Dine (1908) in Honolulu studied fleas that he called ". . . the common dog and cat flea (*Ctenocephalus canis*)." He added the footnote, "*Pulex serraticeps* is a synonym." We are of the opinion that this and the other published reports of *C. canis* could refer to cat fleas. Fig. 20, Plate I, of Fullaway and Krauss (1945) is, however, of a dog flea, but without locality data.

Besides being carried ashore by man himself, *C. f. felis* probably entered the islands many times since 1778 on dogs and cats brought from North America and Europe. If dogs brought to the islands in ancient times by Polynesians from the South Pacific were flea infested, the species was most likely *Ctenocephalides orientis* (Jordan), one not yet recorded in Polynesia. On the other hand, the ubiquitous cat flea became notorious for its outbreaks in Honolulu (Pemberton, 1934) and it is probably the species that commonly attacks man, especially in low lying areas along the shore. Human fleas and dog fleas are not apt to be found in such habitats, but cat fleas thrive there. Thus, *C. f. felis* is likely the "ukulele" of Hawaiians of the nineteenth century and the "Floh" or "flea" referred to by European and American visitors in that era.

The dog, one of the true hosts of the cat flea, held an important place in early Hawaiian civilization (Luomala, 1960). In the subtropical environment well populated with natives and their dogs, the cat flea population could doubtless increase to one of extraordinary size. Early in the twentieth century the dog was definitely identified as an important host of *C. canis* (probably *C. f. felis*). In 1907 Van Dine, a professional entomologist, was engaged in the investigation of outbreaks of these fleas in Honolulu (Smith, 1908). Van Dine (1908) mentioned that several outbreaks of the ". . . common dog and cat flea . . ." occurred in residences, and he commented that homeless cats and dogs occurred in and about the city. One of two particular infestations was traced to dogs sheltering under a house; the other case concerned a family returning after an absence to find their house, yard, and outbuildings infested.

The cat flea is the most widespread flea in the islands. It has no obvious range limitations imposed by either elevation or rainfall. No true hosts from the uppermost slopes of the high mountains, however, have been examined for fleas. The maximum elevation record is 2,379 m in the Puu Kihe Forestry Plot on the northeast slope of Mauna Kea. Extremes of average annual rainfall at collecting localities on the Island of Hawaii are less than 188 mm near Kawaihae Bay to about

4,826 mm at Kaumana.

Seasonal occurrence of *C. f. felis* on female mongooses was rather stable in the Hamakua District where cat flea-mongoose relationships were studied for three years (Haas, 1966a). Month-to-month deviations from the mean of 1.5 fleas per female mongoose were slight. With male mongooses, however, the mean was 4.3 during the mongoose breeding season, December-July, and 2.4 during the nonbreeding season, August-November. Sex ratio on mongooses was relatively stable at about 28% males. In Honolulu, Cole and Koepke (1947b) found that the infestation of *R. norvegicus* was higher in drier than in wetter months.

Hosts of *C. f. felis* are many. True hosts include cat, dog, mongoose, and rabbit. Eskey (1934) did not specify on which island(s) he found infested mice and mongooses. He was first to suggest that mongooses were natural (true) hosts. Additional data by Cole and Koepke (1947b) and Haas (1966a) support his suggestion.

The cat flea-rabbit relationship discovered on Manana Island by Tomich et al. (1968) is of particular interest regarding adoption of new hosts by fleas in historical times. Evidently, this unique flea-host relationship came about only in isolation from carnivores.

6. *CTENOCEPHALIDES CANIS* (CURTIS)

(Figures 15-18)

Pulex canis Curtis, 1826, Brit. Ent. 3:114.
?*Ctenocephalus canis:* Van Dine, 1908, Ann. Rep. Haw. Agr. Exp. Sta. for 1907, pp. 35, 48.--Van Dine & Nörgaard, 1908, Proc. Haw. Live Stock Breeders' Assoc. 5th Ann. Meet., 1907, p. 70.--Van Dine, 1909, Ann. Rep. Haw. Agr. Exp. Sta. for 1908, p. 37.--McCoy & Bowman, 1914, Pub. Hlth. Rep. 29:1634.--Bryan, 1915, Natural History of Hawaii, p. 401.
?*Pulex serraticeps:* Van Dine, 1908, Ann. Rep. Haw. Agr. Exp. Sta. for 1907, p. 35.
?*Pulex canis:* Bryan, 1915, Natural History of Hawaii, p. 401.
?*Ctenocephalides canis:* Fullaway & Krauss, 1945, Common Insects of Hawaii, p. 410, pl. I, fig. 20 (fig. appears to be of *C. canis*).
Ctenocephalides canis: Alicata, 1969, Parasites of Man and Animals in Hawaii, p. 87 (refers to lack of proof of presence in Hawaii).--Haas et al., 1971, Haw. J. Hist. 5:60.--Teeter, 1971, Univ. N. Iowa Quart. 3:16 (photomicrograph of head and thorax of female specimen from Hawaii).

DISTRIBUTION. Cosmopolitan in more temperate regions.

OAHU. Recorded (questionable) by Van Dine (1908) in residences in Honolulu.

HAWAII. Recorded (questionable) by McCoy and Bowman (1914) from rodents along the Hamakua Coast. *ADDITIONAL RECORDS* (confirmed). Humuula, 2,043 m: 1 ♂, abandoned dog shed, Aug. 1968, S. Kaaekuahiwi & E. Auna; 1 ♀, ex *Canis familiaris*, Apr. 1969, P. Q. Tomich.

HOSTS. Recorded from *C. familiaris* and an abandoned dog shed; questionably from *Felis catus, Homo sapiens*, rodents, and in and about houses.

Confusion of the dog flea, *C. canis*, and *Ctenocephalides felis felis* by several authors in the first half of the twentieth century is not unique for the Hawaiian Islands. These old reports of dog fleas will remain questionable unless preserved specimens of the fleas referred to by the authors are located and restudied.

We expected that if a resident population of dog fleas existed, it would be on the upper slopes of the higher mountains, for *C. canis* is not a tropical or subtropical flea. Populations of dog fleas do not persist near sea level on Pacific islands in the tropics. Hopkins (1961) recorded three specimens from a dog on Guam; however, these specimens were reexamined by Wilson (1972) and determined to be *Ctenocephalides orientis*.

As we have confirmed the occurrence of the dog flea in only one locality, namely Humuula, Hawaii, we can only roughly estimate the minimum elevation at which this species can maintain a population. Perhaps it is not far below 2,000 m. Regardless, the high mobility of its host, especially with the aid of man, could account for occasional collections near sea level. Pemberton (1943) stated that dog fleas are frequently introduced on imported dogs. The figure labeled *C. canis* by Fullaway and Krauss (1945) appears to be a dog flea. Therefore, some authors may have had specimens of this species, but we have not located any of them. We believe that the two records from Humuula are the first from the resident *C. canis* population in the usual range of that species. As elevations exceed 2,000 m on Maui, dog fleas also may be established there.

7. *XENOPSYLLA CHEOPIS* (ROTHSCHILD)

(Figures 19-22)

Pulex cheopis Rothschild, 1903, Ent. Mon. Mag. 39:85.
Loemopsylla cheopis: McCoy & Bowman, 1914, Pub. Hlth. Rep. 29:1634.
Xenopsylla cheopis [?partim] : Ewing, 1924, Proc. Ent. Soc. Wash. 26:209, 210.
Xenopsylla cheopis: Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44, 45.--Pemberton, 1926, Proc. Haw. Ent. Soc. 6:221.--Barnum, 1930, Haw. Planters' Rec. 34:422.--Jordan, 1932, Novit. Zool. 38:266.--Eskey, (in Grubbs), 1933, J. Pan-Pacif. Res. Inst. 8:8, 9.--McMullen, 1933, Bull. Mens. Office Internat. Hyg. Pub. 25:1931.--Eskey, 1934, Pub. Hlth. Bull. No. 213:12-45, 48-54, 60-62, 69.--Anonymous, 1935, Pub. Hlth. Rep. 50:255-57.--Wu (in Wu et al.), 1936, Plague: A Manual for Medical and Public Health Workers, p. 275.--Wu et al., 1936, Plague: A Manual for Medical and Public Health Workers, p. 530.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Doolittle, 1941, Ann. Internal Med. 14:2095.--Mumford, 1942, Am. Sci. 30:216.--Carter, 1943, Haw. Med. J. 2:296.--Pemberton, 1943, Haw. Med. J. 2:191.--Mumford & Mohr, 1944, Am. J. Trop. Med. 24 (Suppl.): 14.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 289.--Cole, 1945, Pub. Hlth. Rep. 60:1339-42.--Hampton, 1945, Pub. Hlth. Rep. 60:1366.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Rumreich & Koepke, 1945, Pub. Hlth. Rep. 60:1422-27.--Augustson, 1947, Proc. Haw. Ent. Soc. 13:33, 34, 36.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:20, 25, 26, 28-31, 35-41, 44.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:226.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Mohr, 1951, Am. J. Trop. Med. 31:357-59.--Baldwin et al., 1952, J. Mamm. 33:351.--Hirst, 1953, The Conquest of Plague, p. 182.--Hopkins & Rothschild, 1953, An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History), vol. I, p. 259.--Norris et al., 1953, Pub. Hlth. Rep. 68:803.--Pollitzer, 1954, Plague, pp. 54, 371, 390, 489.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50, 56, 63.--Link, 1955, Pub. Hlth. Monogr. No. 26:76.--Kartman et al., 1956, Bull. Wld. Hlth. Org. 14:681, 682, 687, 694.--Stark & Kartman, 1957, Am. J. Trop. Med. Hyg. 6:707.--von Bormann (in Rodenwalt & Jusatz), 1961, World Atlas of Epidemic Diseases, pt. III, pp. 71, 73, 74.--Gross, 1961, Proc. Ninth Pacif. Sci. Congr. Pacif. Sci. Assoc. 19:53.--Hopkins, 1961, Insects of Micronesia 14:103.--Raettig et al. (in Rodenwaldt & Jusatz), 1961, World Atlas of Epidemic Diseases, pt. III, pp. 25, 26.--Mitchell, 1964, Proc. Haw. Ent. Soc. 18:414, 415.--Haas, 1965, J. Med. Ent. 2:75-82.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 43, 78, 79, 85, 86, 107, 108, 113, 114.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Feb. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 16, 46.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Dec. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 8, 23.--Hinton & Dunn, 1967, Mongooses, p. 108.--Devick, 1968, Asia-Pacif. Interchange Proc., pp. 138-40, 143.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., pp. 273-76, 278, 281.--Muirhead-Thomson, 1968, Ecology of Insect Vector Populations, pp. 107-109.--Samarina et al., 1968, Zool. Zh. 47:266.--Tomich et al., 1968, Pacif. Sci. 22:363.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 204.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 55, 95, 96, 108, 110, 150, 151, 157,

158, 159.--Tomich, 1969, Mammals in Hawaii: a synopsis and notational bibliography, pp. 166, 178.--Kramer, 1971, Hawaiian Land Mammals, p. 133.

DISTRIBUTION. Cosmopolitan.

KAUAI. 1 ♀, ex 7 *Mus musculus*, July 1960, J. T. Kajiwara; 7 ♂♂, 6 ♀♀, ex 6 of 167 *Rattus exulans*, July, Sept., Oct. 1960, Apr. 1961, JTK; 4 ♂♂, 3 ♀♀, ex 3 or more of 78 *Rattus norvegicus*, Feb., Oct. 1960, Jan. 1961, JTK; 1 ♂; 1 ♀, ex 55 *Rattus rattus*, Feb., July 1960, JTK. Kawaihau Dist.: 2 ♂♂, 1 ♀, ex 2 of 35 *R. exulans*, Mar. 1961, JTK; 1 ♀, ex 23 *R. norvegicus*, Mar. 1961, JTK. Koloa Dist.: 1 ♂, ex 5 *M. musculus*, May 1961, JTK; 4 ♂♂, 1 ♀, ex 3 of 65 *R. exulans*, May 1961, JTK. Waimea Dist.: 3 ♂♂, 3 ♀♀, ex 2 of 18 *M. musculus*, July, Dec. 1960, JTK; 19 ♂♂, 20 ♀♀, ex 78 *R. exulans*, June, Dec. 1960, June 1961, JTK; 36 ♂♂, 37 ♀♀, ex 103 *R. norvegicus*, June, Dec. 1960, June 1961, JTK; 6 ♂♂, 5 ♀♀, ex 7 of 73 *R. rattus*, June 1960, June 1961, JTK.

OAHU. Recorded by Pemberton (1925) from rats in Honolulu; recorded by Eskey (1934) from rats in Aiea, Honolulu, Kipapa, Waimanalo, and Waipahu, and from *M. musculus*; recorded (Eskey, 1934) by Anonymous (1935) from rats in Honolulu; recorded by Doolittle (1941) from (*R.*) *norvegicus, alexandrinus*, and *rattus* in Honolulu; recorded by Cole (1945) from rats in Honolulu; recorded by Rumreich and Koepke (1945) from commensal rats in Honolulu; recorded by Cole and Koepke (1947a) from rodents in Honolulu; recorded by Cole and Koepke (1947b) from *Rattus hawaiiensis, R. norvegicus, R. rattus*, and mongooses in Honolulu; recorded by Cole and Koepke (1947c) from rodents in Honolulu; recorded (Cole and Koepke, 1947b) by Mohr (1951) from Norway, roof, and Hawaiian rats in Honolulu; recorded by Hopkins and Rothschild (1953) from brown rat in Wahiaivu (Wahiawa); recorded (Mohr, 1951) by Pollitzer (1954) from Norway rats in Honolulu; recorded by Mitchell (1964) from *R. exulans, R. norvegicus*, and *R. rattus* in Manoa Valley (Honolulu). *ADDITIONAL RECORDS*. Honolulu: 1 ♀, in dwelling, Jan. 1932, C. E. Pemberton; 1 ♂, ex *R. rattus*, Feb. 1941, CEP; 1 ♀, ex *R. norvegicus*, July 1948, C. R. Joyce; 2 ♂♂, 5 ♀♀, ex *R. norvegicus*, Jan. 1953, CRJ; (Kaimuki): 2 ♂♂, 1 ♀, ex *Rattus* sp., Apr. 1940, CEP; 3 ♀♀, ex *M. musculus*, Aug. 1942, Y. Kondo; (Manoa Valley): 3 ♂♂, 3 ♀♀, ex *R. rattus*, Dec. 1940, Dec. 1941, CEP. Tantalus: 1 ♀, ex *R. rattus*, Nov. 1963, D. M. Tsuda & W. J. Voss.

MANANA (1.3 km off SE tip of Oahu). Recorded (Wilson, pers. com.) by Haas (1965a) from *M. musculus*; recorded by Tomich et al. (1968) from *M. musculus* and *Oryctolagus cuniculus*.

MAUI. Recorded by Eskey (1933) from rats in the Makawao Dist.; recorded by Eskey (1934) from rats in Haiku, Kahului, Kailua, Kula, Lower Paia, Makawao, Olinda, Puunene, Upper Paia (Paia), and Wailuku, from *M. musculus* and man; recorded (Eskey, 1934) by Anonymous (1935) from rats in central Maui; recorded (Eskey, 1934) by Bonnet (1948) from rodents in Makawao; recorded by Hopkins and Rothschild (1953) from rats. *ADDITIONAL RECORDS*. Keokea (Kula area): 1 ♂, ex 6 *Herpestes auropunctuatus*, Dec. 1966, W. Garcia. Lahaina area: 1 ♀, ex 17 *R. exulans*, Dec. 1966, WG; 2 ♂♂, 4 ♀♀, ex 16 *R. rattus*, Dec. 1966, WG. Puunene: 3 ♂♂, 8 ♀♀, ex *R. rattus*, May 1934, H. Stein.

HAWAII. Recorded by McCoy and Bowman (1914) from rodents along the Hamakua Coast; recorded (erroneously, at least in part) by Ewing (1924) from *R. rattus* and *R. norvegicus* in Honokaa; recorded by Pemberton (1925) from rats in the Hamakua Dist. and from a mongoose in Honokaa; recorded (Pemberton, 1925) by Barnum (1930) from rats at Honokaa (Hamakua Dist.); recorded by Eskey (1933) from rats in the Hamakua Dist.; recorded by Eskey (1934) from rats in Ahualoa, Hilo, Honokaa, Kalopa, Kukaiau, Kukuihaele, Laupahoehoe, Lower Pohakea, Olaa (Keaau), Onomea, and Pepeekeo, from *M. musculus* in the Hilo sector and the Hamakua Dist., and from man; recorded (Eskey, 1934) by Anonymous (1935) from rats in Hilo and the Hamakua Dist.; recorded (Eskey, 1934) by Hampton (1945) from rodents in the Hamakua Dist.; recorded (Eskey, 1934) by Bonnet (1948) from rodents in Hamakua; recorded by Gross and Bonnet (1951) in the Hamakua Dist.; recorded by Hopkins and Rothschild (1953) from rats in Honakaa (Honokaa); recorded (Eskey, 1934) by Pollitzer (1954) from the Hamakua Dist.; recorded by Kartman and Lonergan (1955) from *R. rattus*, and *R. hawaiiensis* in Kaunamano Gulch and Paauhau, field 1, and from *R. norvegicus* in Kaunamano Gulch; recorded by Kartman et al. (1956) from around Honokaa; recorded by Gross (1961) from *R. hawaiiensis, R. norvegicus* and all other rodent species present in the Hamakua Dist.; recorded by Haas (1965a) from *M. musculus, R. exulans, R. norvegicus*, and *R. rattus* in the Hamakua Dist.; recorded by Devick (1968) from *R. norvegicus*; recorded by Malley and Devick (1968) from *R. norvegicus* and other rodents. *ADDITIONAL RECORDS*. Captain Cook (4.8 km S), 464 m: 2 ♂♂, 1 ♀, ex *R. norvegicus*, Feb. 1963, G. E. Haas. Halaula (Kohala Mill), 76 m: 1 ♀, ex *R. exulans*, Jan. 1962, GEH & T. Ishinaga.

Honokaa: 1 ♂; 1 ♀, ex *R. norvegicus*, Jan., Nov. 1924, CEP; (3 km SW: Ahualoa Homesteads), 610 m: 15 ♂♂, 12 ♀♀, ex *R. norvegicus* nest with rat, Apr. 1963, G. P. Mills & T. Saguicio; (2.7 km SE), 412 m: 1 ♂, 1 ♀, ex *R. exulans* nest, Feb. 1964, W. Mills. Ka Lae (South Cape): 1 ♂, ex *M. musculus*, July 1952, W. Graf. Kawaihae, 3 m: 2 ♂♂, 3 ♀♀, ex 4 *R. rattus*, July, Aug. 1968, S. Kaaekuahiwi & E. Auna; (2 km SE: Makiki Nursery), 72 m: 2 ♀♀, ex 11 *R. rattus*, July, Aug. 1968, SK & EA; (Spencer Park), 3 m: 1 ♂, 5 ♀♀, ex *R. exulans*, July, Aug. 1968, SK & EA; Kukuihaele, 223 m: 2 ♀♀, ex *R. norvegicus* nest with rats, Oct. 1961, N. Wilson; 244 m: 1 ♀, ex *R. exulans* nest with rats, Aug. 1963, WM; 1 ♂, ex *R. exulans* nest, June 1964, WM; (0.8 km NE: camp 104), 171 m: 1 ♂, 4 ♀♀, ex *M. musculus* nest with mice, Jan. 1962, NW; (1.3 km NE), 120 m: 1 ♂, ex *R. ?exulans* nest, Aug. 1962, GEH; (1.9 km ESE), 130 m: 3 ♂♂, ex *M. musculus* nest, Aug. 1963, WM; (1.4 km ESE), 335 m: 1 ♂, 3 ♀♀, ex *R. exulans* nest, June 1964, GPM & TS. Kupaahu, 15 m: 1 ♀, ex *Canis familiaris*, May 1964, GPM & TS. Mahukona, 8 m: 5 ♂♂, 4 ♀♀, ex 2 *R. rattus*, Jan. 1962, GEH & TI; (Kapaa Beach Park), 3 m: 9 ♂♂, 6 ♀♀, ex 1 of 15 *M. musculus*, July, Aug. 1968, SK & EA. Makahalau Camp, 1,171 m: 1 ♂, 2 ♀♀, ex 2 *R. rattus*, Nov. 1962, GEH & GPM. Makapala, 67 m: 1 ♀, ex *M. musculus*, Feb. 1962, GEH & TI; (0.5 km SSW), 146 m: 1 ♀, ex *M. musculus*, Feb. 1962, GEH & TI; (Pololu Valley overlook), 126 m: 1 ♂, ex *M. musculus*, Jan. 1962, GEH & TI; 1 ♂, 1 ♀, ex *R. exulans*, Jan. 1962, GEH & NW. Paauilo (5.6 km SE), 579 m: 1 ♂, 1 ♀,ex *R. exulans* nest, Feb. 1964, WM. Puu Waawaa (ranch headquarters), 842 m: 1 ♀, ex *M. musculus*, Sept. 1963, GEH & GPM; 1 ♂, 2 ♀♀, ex 1 of 11 *R. rattus*, Aug. 1968, SK & EA. Puuanahulu, 665 m: many, ex many *M. musculus*, Sept. 1963, GEH & GPM. Upolu Point (Coast Guard Station), 15 m: 2 ♂♂, 6 ♀♀, ex 19 *M. musculus*, Aug. 1968, SK & EA. Wainaia Gulch (N Kohala Dist.), 38 m: 1 ♀, ex *R. exulans*, Jan. 1962, GEH & TI. Waipio, 8 m: 1 ♀, ex *R. rattus*, Nov. 1961, GEH. Waipio Valley (E rim), 518 m: 1 ♀, ex *H. auropunctatus*, July 1962, SK.

HOSTS. Recorded from bodies and nests of *M. musculus, R. exulans*, and *R. norvegicus*; from bodies of *C. familiaris, H. auropunctatus, Homo sapiens, O. cuniculus*, and *R. rattus*; from dwelling.

The Oriental rat flea, *X. cheopis*, was first recorded by McCoy and Bowman (1914) through specimens collected from rodents trapped along the Hamakua Coast, Island of Hawaii. *X. cheopis* very probably entered the islands on *R. norvegicus* and *R. rattus* that escaped from ocean vessels in 1899 and the early 1900's as the last pandemic of plague would suggest, but introductions earlier in the nineteenth century are highly probable. Islands where this flea most likely will be discovered are Midway, Lanai, and Molokai.

Although occasional specimens are found on rodents and in subterranean nests far from buildings, the Oriental rat flea is most abundant on *R. norvegicus* and in its nests in or under buildings. This flea thrives in extremely dry areas such as Kawaihae (less than 188 mm average annual rainfall) where *Xenopsylla vexabilis* is not found. Shelter from rainfall is favorable regardless of elevation (temperature), at least up to an elevation of 1,171 m at Makahalau. At lower elevations buildings may also afford necessary shelter from excessive heat.

Our data are insufficient to indicate seasonal occurrence of *X. cheopis* on hosts and in their nests. Eskey (1934) reported that the highest infestations of rats caught inside and under buildings were during April-September; the highest infestations of rats caught over 15 m from buildings were during July-December. In Honolulu, Cole and Koepke (1947b) found that abundance on *R. norvegicus* and *R. rattus* had a slight negative correlation with temperature.

The sex ratio of *X. cheopis* on trapped rats received considerable study. Eskey (1934) reported 52% females for his entire study. In winter when infestation was lowest, females increased to 58%. Therefore, believing no change occurred in the sex ratio in the total population, he reasoned that one must assume females are not closely attached to hosts in summer. Cole (1945) studied data from *X. cheopis* and rats in Honolulu (and three North America cities) and concluded that *X. cheopis* males are more sensitive than females to day-to-day temperature changes. The males

shift to rats at high temperatures and from them at low temperatures. Meanwhile, the females remain on their hosts in relatively constant numbers. Therefore, he concluded that an index based on females only may have a more stable relationship to the total flea population.

R. norvegicus is clearly the most heavily infested of the four true hosts of *X. cheopis*, and that it has attributes of a very suitable host was confirmed experimentally (Haas, 1965a). Thus, the declining population of Norway rats in the Hamakua District in the early 1960's may be a factor in the scarcity of *X. cheopis* as compared with conditions in Eskey's (1934) time. He indicated that 17 to 18% of all fleas were *X. cheopis* and about 34% were *X. vexabilis*. In the early 1960's *X. cheopis* was seldom found, even in villages. Eskey's (1934) studies were made during a period of subnormal rainfall and he thought this had a favorable effect on the prevalence of *X. cheopis*. Subnormal rainfall also was a feature of the early 1960's (Haas, 1965b).

On Hawaii, the cane-growing area west of Pololu Valley has a climate similar to that in the enzootic plague area of the Hamakua District; however, in February 1962 *X. cheopis* was the most abundant species of rodent flea despite the apparent absence of *R. norvegicus*. Eskey (1934) reported that except for the Kula zone, central Maui was free of *R. norvegicus*, yet *X. cheopis* was ubiquitous and in six of nine other trapping zones, it was the most abundant rodent flea on the other rats as a group, that is, *R. exulans* and *R. rattus* pooled. Furthermore, in the absence of rats, house mice, despite their inferiority to rats as hosts (Haas, 1965a) can serve as suitable hosts as proved by the house mouse-Oriental rat flea association on Manana Island (Tomich et al., 1968). House mice on Manana have a higher infestation of *X. cheopis* than house mice anywhere else in the Hawaiian Islands.

Eskey (1934) reported that Oriental rat fleas were somewhat more prevalent on young rats than adults and were more prevalent on females than males. However, he pooled data in such a way that it is impossible to know if all three species of rats were hosts in all localities. He did not specify on which island(s) the mongooses were infested. The record of man as a host comes from his inference based on epidemiological evidence from the enzootic plague areas on Maui and Hawaii. He believed that *X. cheopis* was responsible for nearly all cases of human plague.

Records of *X. cheopis* before Eskey's (1934) study are questionable as this flea was confused with *X. vexabilis* prior to the latter's discovery. For example, we have examined seven of the eight specimens Ewing (1924) recorded as *X. cheopis*, and all are *X. vexabilis*. Sometime after Eskey's study in 1932-33, Pemberton, who collected the eight specimens determined by Ewing (1924) in Honokaa in 1922 and 1923, correctly redetermined the seven remaining in the Hawaiian Sugar Planters' Association collection in Honolulu. Specimens collected by Pemberton in 1924 were not listed by Ewing (1924). In January 1924 Pemberton collected a male *X. cheopis* from *R. norvegicus* in Honokaa. The specimen is in the Hawaiian Sugar Planters' Association collection.

8. *XENOPSYLLA VEXABILIS* JORDAN

(Figures 23-27)

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1936, Plague: A Manual for Medical and Public Health Workers, p. 530.--Thompson, 1937, Ent. Mon. Mag. 73:186, 187.--Hegner et al., 1938, Parasitology, p. 638.--Adamson, 1939, Bishop Mus. Bull. 159:59, 68.--Herms, 1939, Medical Entomology, 3rd ed., p. 417.--Mumford, 1942, Am. Sci. 30:216.--Pemberton, 1943, Haw. Med. J. 2:191.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 289.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Augustson, 1947, Proc. Haw. Ent. Soc. 13:33-36.--Chabaud, 1947, Ann. Parasit. Hum. Comp. 22:360, 366.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:28, 29.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:226.--Zimmerman, 1948, Insects of Hawaii, vol. I, Intro., p. 69.--Brumpt, 1949, Précis de Parasitologie, 6th ed., vol. II, p. 1305.--Chandler, 1949, Introduction to Parasitology, 8th ed., pp. 594, 606.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Pollitzer, 1952, Bull. Wld. Hlth. Org. 7:249, 250.--Ioff & Scalon, 1954, Keys to the Fleas of Eastern Siberia, the Far East, and Adjoining Regions, pp. 55, 148, fig. 86g.--Link, 1955, Pub. Hlth. Monogr. No. 26:76.--Kartman et al., 1956, Bull. Wld. Hlth. Org. 14:682.--Rosický, 1957, Blechy--Aphaniptera, p. 195, fig. 61E.--Chandler & Read, 1961, Introduction to Parasitology, 10th ed., pp. 646, 656.--Raettig et al. (in Rodenwaldt & Jusatz), 1961, World Atlas of Epidemic Diseases, pt. III, pp. 25, 26.--Meyer (in Hull), 1963, Diseases Transmitted from Animals to Man, 5th ed., p. 569.--Cheng, 1964, The Biology of Animal Parasites, p. 571.--Jordan (in Smart), 1965, Insects of Medical Importance, 4th ed., p. 238.--Muirhead-Thomson, 1968, Ecology of Vector Populations, p. 108.--Travis et al., 1968, U. S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 204.

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Xenopsylla vesabilis (sic) *hawaiiensis:* Kramer, 1971, Hawaiian Land Mammals, p. 133.

DISTRIBUTION. Southeast Asia (Thailand, Cambodia, and Philippines), Australia (Franklin Island, South Australia, and Queensland), New Guinea, New Zealand (Hen and Little Barrier Islands), Kermadec Islands (Raoul Island), Hawaiian Islands.

KAUAI. 18 ♂♂, 4 ♀♀, ex 3 of 141 *Rattus exulans*, Feb., Mar. 1960, J. T. Kajiwara. Kawaihau Dist.: 3 ♂♂, ex 1 of 63 *R. exulans*, May 1960, JTK. Koloa Dist.: 3 ♂♂, 1 ♀, ex 4 of 78 *R. exulans*, Apr. 1960, JTK. Waimea Dist.: 3 ♀♀, ex 43 *R. exulans*, June 1960, JTK; 1 ♂, 5 ♀♀, ex 90 *Rattus norvegicus*, June, Dec. 1960, JTK.

OAHU. Recorded by Jordan (1932) from rats 9 miles (14.5 km) from Honolulu on the opposite side of the island; recorded by Eskey (1933) from rats in Aiea, Waipahu, and windward side of the Pali; recorded by Eskey (1934) from rats in Aiea, Kipapa, Waimanalo, and Waipahu, and from *Mus musculus*; recorded (Eskey, 1934) by Anonymous (1935) from field rodents; recorded (Jordan, 1932) by Herms (1939) from rats 9 miles (14.5 km) from Honolulu on the opposite side of the island; recorded by Cole and Koepke (1947b) from *Rattus* in Honolulu; recorded (Jordan, 1932) by Herms and James (1961) from rats about 9 miles (14.5 km) from Honolulu on the opposite side of the island. *ADDITIONAL RECORD*. Honolulu (Palolo Valley): 3 ♂♂, 1 ♀, ex *Rattus rattus*, Apr. 1923, O. H. Swezey.

MAUI. Recorded by Jordan (1932) from rats, especially *Rattus hawaiiensis*; recorded by Eskey (1933) from rats in the Makawao Dist.; recorded by Eskey (1934) from rats in Haiku, Kahului, Kailua, Kula, Lower Paia, Makawao, Olinda, Puunene, Upper Paia (Paia), and Wailuku, and from *M. musculus*; recorded (Eskey, 1934) by Anonymous (1935) from field rats in central Maui; recorded (Eskey, 1934) by Wu (1936) in central Maui; recorded (Eskey, 1934) by Bonnet (1948) from rodents in Makawao; recorded by Hopkins and Rothschild (1953) from rats and *Rattus [exulans] hawaiiensis*; recorded (Eskey, 1934) by Link (1955) from domestic rodents; recorded (Eskey, 1934, Jordan, 1932) by Kartman et al. (1956) from *R. hawaiiensis.*

HAWAII. Recorded (as *X. cheopis*) by Ewing (1924) from *R. norvegicus* and *R. rattus* in Honokaa; recorded by Jordan (1932) from rats, especially *R. hawaiiensis*, in Honokaa; recorded by Eskey (1933) from Norway and other rats in the Hamakua Dist. and from rats in the area from Hilo to Laupahoehoe; recorded by Eskey (1934) from rats in Ahualoa, Hilo, Honokaa, Kalopa, Kukaiau, Kukuihaele, Laupahoehoe, Lower Pohakea, Olaa (Keaau), Pepeekeo, and Upper Pohakea, and from *M. musculus*; recorded (Eskey, 1934) by Anonymous (1935) from field rats in the Hamakua Dist.; recorded (Eskey, 1934) by Wu (1936) in the Kamakua (sic) Dist.; recorded (Eskey, 1934) by Bonnet (1948) from rodents in Hamakua; recorded by Gross and Bonnet (1951) from the Hamakua Dist.; recorded by Hopkins and Rothschild (1953) from Hilo and from rats in Honokaa; recorded (Kartman and Lonergan, 1955) by Kartman (1954) from *R. hawaiiensis, R. norvegicus,* and *R. rattus*, in Kaunamano Gulch, Hamakua Dist.; recorded by Kartman and Lonergan (1955) from *R. hawaiiensis, R. norvegicus, R. rattus*, and their nests in Kaunamano Gulch and from *R. hawaiiensis* and *R. rattus* in Paauhau, field 1; recorded (Eskey, 1934) by Link (1955) from domestic rodents in the Hamakua Dist.; recorded by Kartman et al. (1956) from around Honokaa and from *R. hawaiiensis* in the plague-enzootic region, Hamakua Dist.; recorded by Stark and Kartman (1957) from nests of *R. hawaiiensis, R. norvegicus*, and *R. rattus* in the Honokaa area and from *R. hawaiiensis*; recorded by Gross (1961) from all rodent species present in the Hamakua Dist. including *R. hawaiiensis* and *R. norvegicus*; recorded by Meyer (1963) from field rats; recorded by Haas (1965a) from *R. exulans, R. norvegicus, R. rattus*, and *M. musculus* in the Hamakua Dist.; recorded by Haas (1965b) from nests of *M. musculus* and *R. exulans* near Kukuihaele; recorded by Haas (1966b) from *M. musculus*, *R. exulans*, and their nests near

Kukuihaele; recorded by Devick (1968) from *R. exulans*; recorded by Malley and Devick (1968) from *R. exulans* and other rodents; recorded by Haas (1969) from *M. musculus, R. exulans*, and their nests near Kukuihaele and from *R. exulans* nests in other localities from 152 to 305 m in the enzootic plague area, Hamakua Dist. *ADDITIONAL RECORDS*. Haina (1.2 km NW), 60 m: 1 ♂, 2 ♀♀, ex *R. exulans* nest, June 1964, W. Mills. Hawaii Volcanoes National Park (Kipuka Nene), 915 m: 1 ♂, 1 ♀, ex *R. rattus*, Dec. 1961, G. E. Haas. Honokaa: 2 ♂♂, 1 ♀, ex 2 *R. norvegicus*, Nov., Dec. 1922, C. E. Pemberton; 1 ♀; 1 ♀, ex *R. norvegicus*, Feb., Mar. 1923, CEP; 3 ♂♂, 3 ♀♀, ex 3 *R. norvegicus*, Nov. 1924, CEP; 1 ♀; 1 ♀, ex *R. rattus*, Nov. 1922, Feb. 1923, CEP; Honomu, 76 m: 5 ♂♂, 9 ♀♀, ex *R. exulans* nest, Jan. 1967, J. Kanaeholo. Kaapahu Homesteads (Hamakua Dist.), 584 m: 1 ♀; 1 ♀; 1 ♀, ex *Herpestes auropunctatus*, Jan., Aug. 1962, Dec. 1963, S. Kaaekuahiwi. Kahaluu (beach park), 3 m: 1 ♂, ex *R. exulans*, Dec. 1961, GEH. Kalopa Gulch (Hamakua Dist.), 244 m: 1 ♀, ex *H. auropunctatus*, May 1964, SK. Kapulena, 464 m: 5 ♂♂, 4 ♀♀, ex 6 *H. auropunctatus*, Dec. 1961, June, Aug. 1962, SK. Kohala Mill area, 37 m: 1 ♂, 4 ♀♀, ex *M. musculus* nest with mice, Apr. 1966, A. Ramos; 42 ♂♂, 60 ♀♀, ex 5 *R. exulans* nests with 18 rats, Apr. 1966, AR; (1.7 km SW), 326 m: 6 ♂♂, ex 2 *R. exulans*, Jan., Feb. 1962, GEH & T. Ishinaga. Kukaiau Ranch (Iolehaehae Camp), 1,915 m: 2 ♂♂, ex *R. rattus*, Mar. 1964, G. P. Mills & T. Saguicio. Kukuihaele, 223 m: 17 ♂♂, 42 ♀♀, ex *R. norvegicus* nest with rats, Oct. 1961, N. Wilson; 268 m: 1 ♂, ex *H. auropunctatus*, Aug. 1960, SK; (3.1 km SSE), 488 m: 26 ♂♂, 7 ♀♀, ex *R. exulans* nest, June 1961, GEH; (3 km SSW: Hamakua Forest Reserve), 564 m: 1 ♂, ex *R. exulans*, May 1961, GEH & C. M. Wheeler. Ookala: 2 ♂♂, ex *Rattus* sp., Nov. 1945, B. Brookman. Paauhau, 90 m: 6 ♂♂, 1 ♀, ex 4 *M. musculus* nests in subterranean nest boxes, July 1961, GEH; 132 m: 1 ♂; 1 ♀, ex *H. auropunctatus*, Dec. 1961, Sept. 1963, SK; (2.5 km ESE), 75 m: 34 ♂♂, 17 ♀♀, ex *M. musculus* nest with mice, Oct. 1963, GPM & TS; (5.4 km SE), 640 m: 1 ♀, ex *R. exulans* nest, Oct. 1963, WM. Pololu Valley, (0.6 km W), 311 m: 1 ♀, ex *M. musculus*, Jan. 1962, GEH & TI; (0.1 km W), 323 m: 1 ♀, ex *R. rattus*, Jan. 1962, GEH & TI. Puu Waawaa (ranch headquarters) 842 m: 5 ♀♀, ex 21 *M. musculus*, Sep. 1963, GEH & GPM. Wainaia Gulch (N Kohala Dist.), 38 m: 1 ♂, ex *R. exulans*, Jan. 1962, GEH & TI; 1 ♂, 1 ♀, ex *R. rattus*, Jan. 1962, GEH & TI. Waipio Valley, 238 m: 1 ♂, ex *H. auropunctatus*, July 1962, GEH & P. Q. Tomich; 5 m: 1 ♂, under house, Oct. 1969, PQT.

HOSTS. Recorded from bodies and nests of *M. musculus, R. exulans, R. norvegicus*, and *R. rattus*; from bodies of *H. auropunctatus* and *Homo sapiens*, and under house.

The Hawaiian rat flea, *X. vexabilis*, or more properly the Oriental-Pacific rat flea, was first recorded by Jordan (1932) through specimens collected by Eskey in Honokaa and on Maui in 1932. When Eskey (1934) began his study in April 1932, he was the first to detect the species in the islands. Other workers had collected *X. vexabilis* specimens earlier but had misdetermined them as *Xenopsylla cheopis*. We were able to confirm that such confusion applied to most of the specimens collected by Pemberton (Ewing, 1924) in 1922 and 1923 from *R. norvegicus* and *R. rattus* in Honokaa. This example is discussed more fully under *X. cheopis*, but here we point out that the collection and preservation of these specimens of *X. vexabilis* prove that this species was infesting commensal rats in the enzootic plague area of the Hamakua District as early as 21 November 1922. Although retrospective epidemiology is beyond the scope of this paper, in the Hamakua District human plague cases reached the all-time high of 12 (6 in Honokaa) in 1922, but only 1 case occurred in 1923.

Before 1932, *R. exulans* (the original true host of *X. vexabilis* in Hawaii) was thought to be near extinction and specimens were not differentiated from the other species of rats by plague surveillance personnel (Eskey, 1934). According to A. Hart, Sr. (pers. com.), formerly of the Plague Surveillance Laboratory in Honokaa, before Eskey's study Hawaiian rats were classified as young Norway rats. This confusion probably resulted in the absence of records of fleas from *R. exulans* (Ewing, 1924, Buxton and Hopkins, 1927, Buxton, 1928). If *R. exulans* had not been confused with the other rats, *X. vexabilis* probably would have been discovered sooner

because Jordan (1932) expected this rat, if really indigenous, to have a flea of its own.

X. vexabilis is not an endemic flea, but it was probably the only mammal flea inhabiting the islands when Cook arrived in 1778. Undoubtedly, ancient Polynesians sailing from the South Pacific in prehistoric times brought with them *R. exulans* infested with *X. vexabilis*.

Although Jordan (1932) described this flea as a new species, *X. hawaiiensis*, he immediately recognized its close similarity to *X. vexabilis*, which he knew occurred in Australia and New Guinea. He had earlier described *X. vexabilis* from South Australia (Jordan, 1925), but it was not until he studied additional specimens from Queensland that he concluded *X. hawaiiensis* was a subspecies of *X. vexabilis* (Jordan, 1936). More recently *X. vexabilis* was reported from New Zealand (Smit, 1965, Ford-Robertson and Bull, 1966), Kermadec Islands (Smit, 1965), Cambodia (Klein, 1971), Thailand (Sankasuwan et al., 1969), Christmas Island (Traub et al., 1970), and Philippines (Traub et al., 1970). Traub (pers. com., 1972) advised us, "The allusion by Traub et al. (1970) to the occurrence of *X. vexabilis* on Christmas Island (south of Java) refers to the flea described as *X. nesiotes* J. & R., 1908, since Traub was of the impression that this taxon may represent a subspecies of *X. vexabilis*."

Except for the Australian records, these distribution data corroborate archeological facts and theories on migrations of the Polynesian peoples and on the locality of their ancestral home on mainland Asia. The South China-Indochina coastal area is designated as the probable home of ancestors of migrant groups from which Polynesians later branched (Suggs, 1960). As is well known, Polynesians were accompanied by *R. exulans* on at least some of the long voyages between Pacific islands (Tomich, 1969). A missing link is the lack of *X. vexabilis* records for the Marquesas Islands (Stewart, 1935b, Adamson, 1939, Mumford, 1942) and the Society Islands (Stewart, 1935a). Some of the other zoogeographical problems are the absence of *R. exulans* among hosts reported for *X. vexabilis* in Cambodia (Klein, 1971) and the absence of old populations of *R. exulans* (and Polynesians) in Australia (Smit, 1965) where the flea was collected from *Leporillus jonesi* and *Rattus culmorum* (Hopkins and Rothschild, 1953).

For 29 years Hawaiian specimens of *X. vexabilis* were classified as *X. v. hawaiiensis*. Smit (1965) concluded from a study of material from Australia, New Zealand, and a long series of specimens that we collected in the Hamakua District that there was no morphological basis for subspecies and synonymized them all with *X. vexabilis*. This is quite understandable for specimens in New Zealand and the Hawaiian Islands when it is recalled that ancestors of the Maoris and Hawaiians probably left the Marquesas Islands directly and *via* the Society Islands for these localities, respectively, in relatively recent times (Sinoto, 1968). Morphological stability in isolated populations of *X. vexabilis* extends even further back in time as Klein (1971) could find no morphological differences among specimens from Hawaii, New Zealand, and mainland Asia (Cambodia and Thailand).

Islands where *X. vexabilis* seems most likely to be discovered are the *Rattus exulans*-infested islets off the east coast of Oahu and on the main islands of Molokai and Lanai. W. O. Wirtz II (pers. com., 1968) found no fleas on the many *R. exulans* he examined on Kure Atoll.

X. vexabilis is a flea of lowlands. It is most abundant from sea level to about 475 m. Between 610 and 915 m specimens were seldom collected, but relatively lighter survey efforts may be partly responsible. *R. exulans* is scarce between 915 and 1,220 m and unlike the other three murids is unknown above 1,250 m (Banko and Wilson, 1968). As Eskey (1934) noted, the range of *X. vexabilis* seems to be influenced strongly by the range of *R. exulans*. This is peculiar because *R. exulans*

does not generally occur in Australia, and in the Hawaiian Islands *M. musculus* and *R. norvegicus* are true hosts and even *R. rattus* probably qualifies as a true host when it inhabits burrows in places with sufficient moisture.

The record of two males of *X. vexabilis* from a *R. rattus* at Iolehaehae Camp, 1,915 m, requires the support of additional data. This is the only record from above 915 m. *R. exulans* was not found above 763 m on the Kukaiau Ranch. To the west, however, this rat ranged up to 964 m on a foothill of Kohala Mountain, south of Waipio Valley near Kamuela. This is 500 m above the known range of *X. vexabilis* in the adjoining area just east of the valley. Intensive trapping was done there at 464 m, yet only a single male *X. vexabilis* was found. Eskey's (1934) highest record on Hawaii, was from Upper Pohakea, 823 m, near the center of the enzootic plague area. Elsewhere on the island we found *X. vexabilis* as high as 842 m in North Kona District and 915 m in Hawaii Volcanoes National Park.

On Maui, Eskey (1934) reported a few specimens from rats in the Kula trapping zone. This zone ranged from about 762 m to about 1,220 m. He did not specify the exact elevations of his *X. vexabilis* collections, but for his entire study he reported a rapid decrease in prevalence at elevations above 610 m, and he even suspected that a mean wintertime temperature of about 21°C resulted in a lower infestation in winter. We assume that he found *X. vexabilis* only at the lower edge of the Kula zone.

In summary, the maximum elevation record of *X. vexabilis* that we accept is 915 m. Certainly, renewed collecting efforts would cause us to revise this figure upward, but it is questionable that this species can maintain a resident population above 1,220 m.

X. vexabilis does not flourish in microhabitats as dry as those in which *X. cheopis* thrives (Eskey, 1934, Stark and Kartman, 1957). In its known range, at least where average annual rainfall is less than 2,540 mm, it is primarily a flea of subterranean nests and burrows that are not sheltered by buildings. In the relative dryness of Honolulu, Eskey (1934) could not find specimens and Cole and Koepke (1947b) could find only 12 specimens among 41,402 fleas collected from rats. Eskey (1934) remarked that he was able to collect specimens in windward central Maui (Kahului and Puunene) where there is less rainfall than in Honolulu. Kahului and Puunene receive an approximate average annual rainfall of only 419 mm. As he suspected, however, air over central Maui has a higher average percent relative humidity than air over Honolulu.

As for the detrimental effects of high rainfall, Eskey (1934) reported that in wet areas such as the Hilo trapping sector (Laupahoehoe-Hilo-Olaa) the index was rather low and 71% of his specimens were females. Olaa is the wettest locality with an average of about 3,683 mm of rainfall per year.

Seasonal occurrence of *X. vexabilis* on trapped rats was more stable on *R. exulans* than on the other two species (Eskey, 1934). Superior host suitability (Haas, 1965a) may be a factor, but a good reason is that *R. exulans* populations are the most stable of all rodent populations in Hawaii (Tomich, ms).

After Eskey (1934) pooled his data from all rats trapped on Maui and in the Hamakua District, he found the highest indices during October-December, the lowest during April-June, and intermediate indices during January-March and July-September. He found the highest *X. vexabilis* infestations of *R. exulans* in July-December and the lowest during January-June, especially April-June.

The Plague Research Unit had several study sites in the Hamakua District. The highest infestations of trapped *R. exulans* were at two of the lowest sites. One was between 76 and 183 m in irrigated cane field 001 of the Paauhau Sugar Co., and the other was between about 122 and 244 m along the east edge of Kahaupu Gulch. Both sites are near Paauhau. However, because plague was more recently detected in

the Kukuihaele area, more intensive studies were conducted there in Honokaa Sugar Co. cane field 101b, particularly between 270 and 299 m. This field is well within the elevation-temperature range of *X. vexabilis*. The flea was present throughout growth of cane crops of 1959-1961 and 1961-1963 in small to moderate numbers. Nest studies provided evidence that breeding occurred in all months at Kukuihaele (Haas, 1966b, 1969).

In the Paauhau area, a high peak in the infestation of trapped *R. exulans* almost always occurred in August-November with sometimes a secondary peak in February-March, 1958-1963. In the Kukuihaele area, the 1961-1963 data indicated peak infestations in November 1961-January 1962 (before nesting in the field by *R. exulans*) and June and November 1962 (Haas, 1969). Fleas were least numerous in February-March and September 1962 and January-March 1963. Including data back to September 1958, *R. exulans* from Kukuihaele had the highest *X. vexabilis* infestations during October-December with secondary peaks during June-July.

Nests of *R. exulans* on the average are more heavily infested with *X. vexabilis* than are the rats caught alive in traps. Trapping rats for determination of flea indices is considerably easier than excavating burrows for fleas in nests. Estimating that proportion of the entire flea population that is in nests only from knowledge of mean numbers of fleas on trapped rats is conjectural as only preliminary quantitative data from the Kukuihaele area are available (Haas, 1969). From 1961-1964 a distinct seasonal cycle occurred in *X. vexabilis* in *R. exulans* nests in the Hamakua District, from 152 to 305 m (241 m average), with a peak in June and a low in January. In cane field 101b at Kukuihaele, 278-299 m, a peak occurred in January as well as July (Haas, 1969). Predominance of females during a wintertime increase in population size suggested that during about three months in midwinter (mean soil temperature below 19 or 20°C) low temperature became a detrimental factor. The effect was to depress the peak of January 1963 at the expense of the males. Apparently mortality was increased or development of immature stages was delayed relative to females. To modify Eskey's (1934) hypothesis, we may say that when males have declined below 45% of the *X. vexabilis* population in *R. exulans* nests, conditions during the preceding weeks have not been entirely favorable for an increase in the total numbers of *X. vexabilis*. For house mouse nests the corresponding value would be about 55%.

According to nest-box studies at Kukuihaele, the seasonal occurrence of *X. vexabilis* in *R. exulans* nests appeared to be under the influence of the rats (their breeding, mortality, migrality, social behavior) primarily and the seasonal changes in temperature secondarily (Haas, 1969). Doubtless, seasonal changes of the climate influenced the hosts, for *R. exulans* has distinct annual cycles of reproduction and abundance (Tomich, ms). Changes in cane plants as they grew also affected these rats in ways of significance to fleas, i.e., nesting habits (Haas, 1969). After *R. exulans* became a nesting resident of the cane field proper, fleas in the field were vitally affected by being exposed to ever changing quantities and qualities of rats in nests and by being in nests which themselves were changing in quantity and quality.

These changes in the rat population and in the rat nests directly affected flea breeding. For example, when there was a declining mean number of rats per nest prior to the summertime wave of parturition, as in late winter of 1961-1962, there was a concentration of actively feeding and breeding fleas on those hosts remaining. This set the stage for an increase in the mean number of fleas per nest a month or so later and was especially noticeable when reinforced by a concurrent wave of maturation of young rats on a per nest basis. Mature *R. exulans* are more suitable for feeding and breeding by *X. vexabilis* than weanlings (Haas, 1965a). Also mature males ranked ahead of mature females.

Chronological changes in the size and quality of the *X. vexabilis* population in each nest of *R. exulans*, as the nest ages, are suggested by data (Table 3) obtained from the nest-box studies (Haas, 1969). In particular, a large number of larvae hatched during the first month, and by the second month many of these larvae had pupated. A relatively slight population shift from larvae to adults was evident between the second and third months, but by the last month of any series, larvae were found in only a sixth of the nests. Qualitative changes in the microhabitat as the nest ages are clearly of importance in the ecology of *X. vexabilis*.

Table 3. Composition of *Xenopsylla vexabilis* populations according to percentages of adults and larvae in infested nests of *Rattus exulans* and *Mus musculus* as the nests aged in subterranean nest boxes in cane field 101b, Kukuihaele, Hawaii, January 1962-March 1963[1]

No. of nests and percent of fleas	Nest inhabitant and month of observation							
	Rattus exulans				*Mus musculus*			
	1	2	3	last[2]	1	2	3	last[3]
Nests	29	18	12	12	41	15	6	7
Fleas								
Adults only	52	61	67	83	68	53	67	57
Adults + larvae	41	28	25	17	27	47	33	43
Larvae only	7	11	8	0	5	0	0	0

[1]Larvae presumed to be all *X. vexabilis* or mixed with a few specimens of *Leptopsylla segnis*.

[2]Last in a series of 3-7 consecutive monthly observations.

[3]Last in a series of 3-6 consecutive monthly observations.

M. musculus is a much less suitable host than *R. exulans* (Haas, 1965a). Nevertheless, the house mouse was usually the most abundant rodent in cane field 101b near Kukuihaele in the early 1960's, and it ranked as the second most important host after *R. exulans*. In fact, despite the scarcity of fleas on trapped individuals, examination of their nests revealed numerous *X. vexabilis* so that mice occasionally supported a higher total population of these fleas than did *R. exulans* (Haas, 1966b). Thus, *M. musculus* served as a suitable host for rat fleas. The seasonal occurrence of *X. vexabilis* in mouse nests in field 101b reached its highest peak in July and August and had a secondary peak in December (Haas, 1969).

An increase in the mean number of mice (nestlings excluded) per occupied nest appeared to favor an increase of the flea population in mouse nests provided that the fleas were allowed a month to develop. In rat nests the comparable relationship was not strong (Haas, 1969). However, quantities of animals in mouse and rat nests were not equal. The mean number of fleas in mouse nests had a smaller and lower range, and the mean number of mice in nests had a higher range (Haas, 1966b, 1969). Furthermore, a comparison of infestation data from mouse and rat nests (Table 3) suggests that despite the similarity in the third month, which has the smallest sample of mouse nests, oviposition and larval growth were sluggish in nests of *M. musculus* and rapid in nests of *R. exulans*. This interpretation is supported by experimental determinations that feeding and breeding rates on *M. musculus* were much lower than on *R. exulans* (Haas, 1965a).

The foregoing discussion may serve as an introduction to the variations of *X.*

vexabilis population sizes in space and time and according to species, sex, and age of host animal, and according to age and "species" of nest. If such heterogeneous data are pooled, the sum total can be influenced according to weight various factors receive. In other words, the apparent seasonal abundance easily can be a biased view of the real area-wide as well as local abundance.

Eskey (1934) was not unaware of problems of heterogeneity, but he pooled species of rats trapped in each locality. It is impossible to know if all three species were infested in all localities. He was first to record the mongoose as a host, but he did not specify on which island(s) the infested mongooses were trapped. The record of man as a host comes from his inference based on epidemiological evidence from the enzootic plague areas on Maui and Hawaii. He believed, however, that most cases of human plague resulted from bites of *X. cheopis* and that *X. vexabilis* was mainly responsible for perpetuation of plague among field rats living away from buildings in rural areas. Using a virulent strain of *Yersinia pestis* from Maui, the vector efficiencies of these two species of fleas were compared experimentally and it was concluded that *X. cheopis* (San Francisco strain) had about twice the efficiency of *X. vexabilis* (Hamakua strain) (Kartman et al., 1956).

RHOPALOPSYLLIDAE

9. *PARAPSYLLUS LAYSANENSIS* WILSON, n. sp.

(Figures 28-31, 33)

Parapsyllus sp.: Haas et al., 1971, Haw. J. Hist. 5:71.

DIAGNOSIS. *P. laysanensis* belongs to the *longicornis*-group and is distinguished from the seven other members in this group by the shape of the median dorsal lobe (m.d.l.), distal-lateral lobe (d.l.l.), and crochet (cr.) of the aedeagus in the male, and sternum VII (st.VII) and spermatheca in the female.

DESCRIPTION. *Head* (Fig. 28): Frontal tubercle (fr.tub.) typically arrowhead-shaped, varying in extent of projection and sharpness of tip, arising low in frontoclypeal region; frontal row of 1 to 3 long setae; ocular row of 3 long setae, all longer than setae of frontal row, 2 in front of sinuate eye, 1 near genal margin reaching up to 3rd segment of maxillary palp; several short setae above last large seta of ocular row and above eye; 0 to 2 short setae between upper 2 long setae of ocular row. Genal process (gen.pro.) short and broad, with 5 to 7 short setae near or on ventral margin. Postantennal region with occipital row of 3 or 4 setae, ventralmost seta much longer than others; 2 or 3 long setae above antennal groove; 5 to 11 short setae in irregular row bordering dorsal margin of antennal groove. Maxillary palp 4-segmented. Labial palp 5-segmented, extending to middle of trochanter. Longest seta of 2nd antennal segment reaching to 3rd segment of club.

Thorax (Fig. 28): Pro-, meso-, and metanotum with 1 row of 7 to 9 setae on each side (excluding intercalary setae); pseudosetae absent. Mesepisternum with 1 seta; mesepimeron with 1 seta. Metepisternum with 1 seta; metasternum without setae; metepimeron with 2 rows of setae, 2 to 4 in anterior row, 5 to 8 in posterior row, setae of posterior row may be irregularly arranged and of different lengths.

Legs (Fig. 28): Mid and hind tibiae each with 5 notches in posterior (dorsal) margin, with 2 setae in each notch; apical notch of mid and hind tibiae with 4 setae. Fore and mid tibiae with 1 apical seta longer than tarsal segment I. Hind tarsal segments II and III with at least 1 apical seta as long as or longer than succeeding segment. Fore tarsal segment V, and mid and hind tarsal segments I longest. Segment V of all tarsi with 3 or 4 pairs of lateral plantar setae, 7 with 3 pairs, 30 with 4 pairs,

10 with 7 setae; 1 pair of pre-apical plantar hairs; 2 pairs of pre-apical plantar setae, 1 with 1 seta; 0 to 5 short plantar setae in area of last pair of lateral plantar setae, 5 with 0, 22 with 1, 11 with 2, 5 with 3, 3 with 4, and 1 with 5 setae, males averaged over 1 seta more than females; 6 of 47 tarsi with 1 plantar hair in area of lst 2 pairs of lateral plantar setae.

Abdomen (Fig. 30): Terga I to VI with 2 rows of setae and circular spiracular fossae, main (posterior) row with 8 or 9 long setae alternating with shorter ones and preceded by somewhat irregular row of 6 to 9 shorter setae; tergum VII (t.VII) with similar setae but not in discernable rows; lowest seta in each row (except on tergum I) below level of spiracle. Sterna II to VII with 9 to 19 long setae, of variable length.

Modified abdominal segments. Male (Figs. 29, 31): Sternum VIII apical margin broadly rounded, with 15 to 20 long setae on ventral part. Apodeme of tergum IX (a.t.IX) rather narrow, without anterior lobe. Manubrium (man.) narrow and slightly curved dorsally, with upturned rounded apex. Body of clasper (b.cl.) quadrangular, with distinct surface sculpture, about 30 long setae on and near dorsal and posterior margins, about 20 long setae dorsoapically on inner surface; group of 2 to 5 setae anterior to acetabulum (acet.) near base of manubrium, occasionally 1 or 2 setae posterior to this group and anterior to base of acetabulum. Movable process (m.p.) elongate, rounded at apex, with about 20 short setae on dorsoapical one-fourth of anterior margin, posterior margin, and mid-portion (both sides), anterior margin slightly angulate with denticulus in middle. Proximal arm of sternum IX (p.a.st.IX) sharply to bluntly hooked anteriorly at apex, with broadly rounded anterior lobe; distal arm of sternum IX (d.a.st.IX) elongate and triangular, gradually tapering to rounded apex, 17 or 18 short, mostly marginal setae on apical one-third, more setae ventral than dorsal, midventral margin in area of anteriormost seta slightly convex. Aedeagal apodeme extends slightly anterior to manubrium, a single penis rod makes one-quarter revolution anterior to aedeagal apodeme; other structures as illustrated.

Female (Figs. 30, 33): Sternum VII lacking sinus, posterior margin extended as narrow lobe, somewhat variable as illustrated, with irregular row of 7 to 10 mostly long setae preceded by 4 to 9 shorter setae. Sternum VIII (st.VIII) small, somewhat narrow and broadly rounded posteriorly, with 3 to 6 minute marginal or submarginal setae on apex, occasionally 1 seta shifted antero-dorsally. Tergum VIII (t.VIII) well developed, slightly lobed dorsocaudally, with sinuate posterior margin, chaetotaxy as indicated. Sternum VIII and tergum VIII with distinct surface sculpturing. Anal stylet (an.sty.) about twice as long as maximum width. Duct of bursa copulatrix (d.b.c.) thick-walled, upper one-fourth curved anteriorly. Bulga (bu.) of spermatheca oval; hilla (hi.) longer than greatest length of bulga, curved, slightly constricted at entrance to bulga.

Length: Male 1.96 to 2.06 mm; female 2.41 to 3.18 mm.

DISTRIBUTION. Hawaiian Islands.

LAYSAN. *Holotype* male (**BISHOP 8818**), ex *Diomedea immutabilis* nest, 8 Dec. 1963, N. Wilson. *Allotype* female, ex *D. immutabilis* nest, 9 Dec. 1963, NW. *Paratypes*: 3 of 5 ♀♀, ex *D. immutabilis* nest, 6 Dec. 1963, NW; 2 ♂♂, 5 of 6 ♀♀ (holotype selected from this series); 1 ♂, 1 of 2 ♀♀; 1 ♀, same data as holotype; 2 ♀♀; 1 ♀, ex *Puffinus pacificus* nest, 9 Dec. 1963, NW. *Additional specimens*: those listed above with paratypes; 3 ♀♀ (unmounted), ex *P. pacificus* nest, 8 Dec. 1963, NW. Some of the above specimens were damaged in the process of remounting and the worst of these were not designated as paratypes. Holotype, allotype, and several paratypes and additional specimens in Bernice P. Bishop Museum collection; other paratypes and specimens in collections of various institutions and colleagues.

HOSTS. Recorded from nests of *D. immutabilis* and *P. pacificus*.

P. laysanensis shares its closest relationship with *Parapsyllus taylori* Jordan, a species known from several islands off the coast of southwestern and southeastern Australia. The aedeagus in *P. laysanensis* has the median dorsal lobe broader and not as strongly flexed ventrally and the distal-lateral lobe of a slightly different shape (Figs. 31, 32). Also the crochet is shorter and not as strongly hooked at the apex (Figs. 31, 32). Females of the two species are very similar with slight differences in the shape of sternum VII and spermatheca (Figs. 33, 34).

The genus *Parapsyllus* is best known from the southern hemisphere, where it is widely distributed over the southern oceans, especially in the New Zealand and Australian subregions (Dunnet, 1964). Smit (1970) recently described a new species from the Galápagos Islands and considerably extended the range of the genus northward. The closest previous record was from Zapalla (north of Valparaiso), Chile (Jordan, 1942). The majority of species and records are from sea birds which nest in burrows or on the surface of the ground.

Our specimens were found by slowly and tediously turning sand in nests of the Laysan albatross and wedge-tailed shearwater. Five additional fleas escaped, including a pair in copulo.

Smit (1964) believes that specimens of *Parapsyllus* are regularly carried by sea birds from one island to another although the chances are slim for the establishment of a new population. Nevertheless, specimens reached Laysan, probably by this method and probably on a species of *Puffinus*. *Puffinus* is widespread throughout the Pacific and includes species which migrate great distances both north and south. *P. pacificus* (nest) is recorded as a host for both *P. laysanensis* and *P. taylori*.

CERATOPHYLLIDAE

10. *NOSOPSYLLUS FASCIATUS* (BOSC)

(Figures 35-37)

Pulex fasciatus Bosc, 1800, Bull. Sci. Soc. Philom. Paris 2:156.
Ceratophyllus fasciatus: Eskey, 1934, Pub. Hlth. Bull. No. 213:13.--Anonymous, 1935, Pub. Hlth. Rep. 50:256.
Nosopsyllus fasciatus: Eskey, 1934, Pub. Hlth. Bull. No. 213:13, 14, 16-18, 46, 47, 53, 55, 59.--Anonymous, 1935, Pub. Hlth. Rep. 50:256.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Pemberton, 1943, Haw. Med. J. 2:191.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 289.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p. 14.--Rumreich & Koepke, 1945, Pub. Hlth. Rep. 60:1422.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:31.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 43, 78, 79, 85, 86, 107, 108, 113, 114.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., pp. 274, 281.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 201.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 55, 95, 96, 108, 110, 150, 151, 158, 159.--Kramer, 1971, Hawaiian Land Mammals, p. 133.
Nosopsyllus (Ceratophyllus) fasciatus: Buxton, 1941, Bull. Ent. Res. 32:121.
Nosopsylla fasciata: Bonnet, 1948, Proc. Haw. Ent. Soc. 13:227.

DISTRIBUTION. Cosmopolitan.

OAHU. Recorded by Rumreich and Koepke (1945) from a commensal rat and by Cole and Koepke (1947b) from *Rattus* sp. in Honolulu.

MAUI. Recorded by Eskey (1934) from rats in Haiku, Kahului, Kailua, Kula, Lower Paia, Makawao, Olinda, Puunene, and Upper Paia (Paia); recorded (Eskey, 1934) by Pemberton (1943); recorded by Simmons et al. (1944) from rats; recorded by Pemberton (1945) from rats; recorded (Eskey, 1934) by Bonnet (1948) from rats in the Kula region; recorded (Pemberton, 1945) by Alicata (1967) from rats. *ADDITIONAL RECORDS*. Kipahulu Valley, 991 m: 1 ♂, ex *Rattus*

exulans, Aug. 1967, N. Wilson; 1 ♂; 1 ♀, ex *Rattus rattus*, Aug. 1967, NW; 1,982 m: 3 ♀♀, ex 2 *R. rattus*, Aug. 1967, NW.

HAWAII. Recorded by Eskey (1934) from rats in Ahualoa, Honokaa, Kalopa, Kukaiau, Kukuihaele, Laupahoehoe, Lower Pohakea, Olaa (Keaau), S Hilo Dist., and Upper Pohakea; recorded (Eskey, 1934) by Pemberton (1943); recorded by Simmons et al. (1944) from rats; recorded by Pemberton (1945) from rats; recorded by Gross and Bonnet (1951) in the Hamakua region; recorded by Kartman and Lonergan (1955) in the Hamakua Dist., recorded (Pemberton, 1945) by Alicata (1967) from rats; recorded by Malley and Devick (1968) from rodents. *ADDITIONAL RECORDS*. Halepiula, 1,769 m: 1 ♀, ex *Rattus norvegicus*, Feb. 1964, G. P. Mills & T. Saguicio. Hawaii Volcanoes National Park (Kipuka Puaulu (Bird Park)), 1,220 m: many, ex 3 *R. rattus*, Mar., Apr. 1965, R. Y. W. Lee; (Namakani Paio campground), 1,205 m: many, ex 2 *R. rattus*, Apr. 1965, RYWL. Honokaa (3 km SW: Ahualoa Homesteads), 610 m: 1 ♂, 1 ♀, ex *R. norvegicus* nest with rat, Apr. 1963, GPM & TS; (2.6 km S: Hamakua Forest Reserve), 595 m: 2 ♀♀, ex *R. exulans* nest, Apr. 1964, GPM & TS. Kaapahu Homesteads (Hamakua Dist.), 720 m: 1 ♂, 2 ♀♀, ex *Herpestes auropunctatus*, Dec. 1961, S. Kaaekuahiwi. Kahawailiilii Gulch (N slope Mauna Kea), 1,598 m: 1 ♀, ex *R. rattus*, Feb. 1964, GPM & TS. Kapulena, 476 m: 1 ♂, ex *H. auropunctatus*, Aug. 1962, SK. Keanakolu (hunters' cabin), 1,613 m: 1 ♂, 3 ♀♀, ex 2 *R. rattus*, July 1968, SK & E. Auna; (Parker Ranch Station), 1,650 m: 1 ♂, 3 ♀♀, ex 5 *R. norvegicus*, July 1968, SK & EA; (ranger station), 1,610 m: many, ex *Mus musculus*, Feb., Mar. 1964, GPM & TS. Kilauea Military Camp area, 1,220 m: 1 ♂, ex *R. norvegicus*, Apr. 1965, RYWL. Kohala Mtn. (E slope Haloa), 964 m: 1 ♂, ex *M. musculus*, Apr. 1964, GPM & TS; 1 ♂, 2 ♀♀, ex *R. exulans*, May 1964, GPM & TS. Kukaiau Ranch (Iolehaehae Camp), 1,915 m: many, ex *M. musculus*, Mar. 1964, GPM & TS; 1 ♂, 1 ♀, ex *R. rattus*, Mar. 1964, GPM & TS; (stone corral), 1,586 m: many, ex *R. norvegicus*, Feb., Mar. 1964, GPM & TS; 1 ♂, 2 ♀♀ ex *R. rattus*, Mar. 1964, GPM & TS; Kukuihaele (3.1 km SSE), 488 m: 1 ♂, 1 ♀, ex *R. exulans* nest, June 1961, G. E. Haas; (2.5 km SSW), 496 m: 1 ♂, 5 ♀♀, ex *R. exulans* nest with dead rat, Aug. 1962, GEH; (3 km SSW: Hamakua Forest Reserve), 564 m: many, ex *M. musculus*, Mar., June, Aug. 1961, GEH & C. M. Wheeler; many, ex *R. exulans*, Mar.-Sept. 1961, GEH & CMW; 5, ex *R. norvegicus*, Mar., Apr. 1961, GEH & CMW; many, ex *R. rattus*, Mar., May, June, Sept. 1961, GEH & CMW. Makahalau Camp, 1,171 m: 2 ♂♂, 6 ♀♀, ex 4 *R. rattus*, Nov. 1962, GEH & GPM. Mana, 1,074 m: 3 ♂♂, 7 ♀♀, ex *R. rattus*, Nov. 1962, GEH & GPM. Paauilo (5.4 km SE), 640 m: 5 ♂♂, 11 ♀♀, ex *R. exulans* nest, Oct. 1963, W. Mills; (5.0 km ESE), 473 m: 4 ♂♂, 4 ♀♀, ex *R. exulans* nest, Dec. 1963, WM; (5.6 km SE), 579 m: 12 ♂♂, 13 ♀♀, ex *R. exulans* nest, Feb. 1964, WM. Palihooukapapa, 1,269 m: 1 ♂, 1 ♀, ex *R. norvegicus*, Nov. 1962, GEH & GPM; 3 ♀♀, ex *R. rattus*, Nov. 1962, GEH & GPM. Pohakuloa, 1,983 m: 1 ♂; 1 ♂, ex *M. musculus*, July 1962, W. Graf. Puu Keanui cinder cone (N Kona Dist., Puu Lehua Quadrangle), 1,594 m: 1 ♀, ex *M. musculus*, Jan. 1963, GEH. Puu Kihe (NE slope Mauna Kea, forestry plot), 2,379 m: 2 ♂♂, ex *M. musculus*, Feb. 1964, GPM & TS; (NE slope Mauna Kea, cabins), 2,364 m: 2 ♂♂, 5 ♀♀, ex 4 *R. rattus*, July 1968, SK & EA. Puu Waawaa (ranch headquarters), 839 m: 1 ♀, ex *R. rattus*, Aug. 1968, SK & EA. Umikoa (Kukaiau Ranch Headquarters), 1,068 m: 2 ♀♀, ex *R. norvegicus*, Feb. 1964, GPM & TS; 3 ♀♀, ex *M. musculus*, July 1968, SK & EA.

HOSTS. Recorded from bodies and nests of *R. exulans* and *R. norvegicus*; from bodies of *M. musculus, H. auropunctatus*, and *R. rattus*.

The northern rat flea, *N. fasciatus*, was first recorded by Eskey (1934) from specimens collected in 1932-1933 in several localities on Maui and Hawaii. This species probably entered the Hawaiian Islands in the nineteenth century or earlier on *R. norvegicus* and *R. rattus* that left ships calling at Hawaiian ports. The island where this flea is most likely undiscovered is Molokai. During a murine typhus survey on Kauai by the Hawaii Department of Health in 1960-1961, J. T. Kajiwara (unpublished) found *Leptopsylla segnis*, but not *N. fasciatus* on rats trapped at higher elevations.

N. fasciatus shows more aversion to higher temperatures than *L. segnis*, very rarely being found near sea level. In the Hamakua District, occasional specimens were found on rodents as low as 366 m in winter. The maximum elevation record

was 2,379 m at Puu Kihe, but the species probably ranges as high as its hosts occur. In subterranean nests the lowest elevation record is 473 m near Paauilo. The specimens were in a *R. exulans* nest excavated from a burrow in December.

Average annual rainfall up to 2,743 mm seems to be unimportant in the geographic distribution of *N. fasciatus*. This flea ranges into the dry area of Pohakuloa where the approximate average annual rainfall is slightly below 508 mm. Eskey (1934) recorded a specimen from Olaa (3,683 mm of rainfall), which is probably at too low an elevation for a resident population. Our records indicate a resident population in the area southwest of Kukaiau, which has an average annual rainfall of about 2,743 mm.

Seasonal occurrence of *N. fasciatus* in nests is unknown. On trapped rats Eskey (1934) reported the heaviest infestation during the "winter" months, especially at elevations below 762 m. At higher elevations in the Kula zone on Maui, he found lesser but still considerable numbers during "spring" and "summer".

True hosts of *N. fasciatus* are probably *R. exulans, R. norvegicus*, and *R. rattus*, and possibly *M. musculus*, although nests of the latter two species have not been recorded as being infested with northern rat fleas. Eskey (1934) reported that this flea was rarely found on mice. On the contrary, we found them common on mice trapped in a *Eucalyptus* plantation 3 km SSW of Kukuihaele, 564 m, during March-June 1961. For example, in May the average number of *N. fasciatus* on 111 mice was 1.4, and on the 58 mice (52%) that were infested, the average was 2.7. Four *R. exulans* and five *R. rattus* trapped in the same plantation at the same time had indices of 3.3 and 2.0, respectively.

Eskey (1934) pooled species of rats in each locality, so it is impossible to know if all three species were infested in all localities. He did not specify whether infested *M. musculus* and *H. auropunctatus* were on Maui, Hawaii, or both islands.

LEPTOPSYLLIDAE

11. *LEPTOPSYLLA SEGNIS* (SCHÖNHERR)

(Figures 38-40)

Pulex segnis Schönherr, 1811, Kongl. Vet. Akad. Nya. Handl. 32:98.
Ctenopsyllus misculi (sic): Ewing, 1924, Proc. Ent. Soc. Wash. 26:210.
Ctenopsyllus musculi: Ewing, 1924, Proc. Ent. Soc. Wash. 26:210.--Pemberton, 1925, Bull. Exp. Sta. Haw. Sugar Planters' Assoc. Ent. Ser. Bull. No. 17:44.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Feb. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, pp. 7, 30.
Leptopsylla musculi: Eskey, 1934, Pub. Hlth. Bull. No. 213:13.--Anonymous, 1935, Pub. Hlth. Rep. 50:256.--Wu et al., 1936, Plague: A Manual for Medical and Public Health Workers, p. 530.
Leptopsylla segnis: Eskey, 1934, Pub. Hlth. Bull. No. 213:13, 14, 16-18, 47, 48, 53, 55, 59.--Anonymous, 1935, Pub. Hlth. Rep. 50:256.--Thompson, 1937, Ent. Mon. Mag. 73:186.--Pemberton, 1945, Proc. Haw. Acad. Sci. 16th Ann. Meet. 1940-41, p.14.--Rumreich & Koepke, 1945, Pub. Hlth. Rep. 60:1422.--Cole & Koepke, 1947, Pub. Hlth. Rep. Suppl. 202:31.--Bonnet, 1948, Proc. Haw. Ent. Soc. 13:227.--Gross & Bonnet, 1951, Pub. Hlth. Rep. 66:1542.--Baldwin et al., 1952, J. Mamm. 33:351.--Kartman & Lonergan, 1955, Bull. Wld. Hlth. Org. 13:50, 66.--Gross, 1961, Proc. Ninth Pacif. Sci. Congr. Pacif. Sci. Assoc. 19:53.--Alicata, 1967, Haw. Agr. Exp. Sta. Tech. Bull. No. 61:42, 78, 79, 85, 107, 108, 114.--Haw. Ent. Soc. Committee Common Names Hawaiian Insects, Dec. 1967, Preliminary List of Common Names of Hawaiian Insects and Organisms, p. 4.--Malley & Devick, 1968, Asia-Pacif. Interchange Proc., p. 281.--Alicata, 1969, Parasites of Man and Animals in Hawaii, pp. 54, 95, 96, 110, 150, 151, 159.--Haas, 1969, Pacif. Sci. 23:72.--Kramer, 1971, Hawaiian Land Mammals, p. 133.

Ctenopsyllus segnis: Pemberton, 1943, Haw. Med. J. 2:191.--Simmons et al., 1944, Global Epidemiology, vol. I, pt. 2, p. 290.--Travis et al., 1968, U.S. Army Natick Labs. Tech. Rep. 68-61-ES, p. 199.

Leptopsylla (Leptopsylla) segnis: Hopkins & Rothschild, 1971, an Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History), vol. V, p. 186.

DISTRIBUTION. Cosmopolitan.

KAUAI. ?Kokee: 4 ♂♂, ex 18 *Rattus exulans*, Oct. 1960, J. T. Kajiwara; 60 ♂♂, 54 ♀♀, ex 15 *Rattus norvegicus*, Oct. 1960, JTK; 2 ♂♂, 8 ♀♀, ex 3 of 21 *Rattus rattus*, Oct. 1960, JTK. Waimea Dist.: 2 ♂♂, ex 13 *R. norvegicus*, June 1961, JTK.

OAHU. Recorded by Rumreich and Koepke (1945) from commensal rats and by Cole and Koepke (1947b) from *Rattus* sp. in Honolulu.

MAUI. Recorded by Eskey (1934) from rats in Haiku, Kahului, Kailua, Kula, Lower Paia, Makawao, Olinda, and Upper Paia (Paia), and from *Mus musculus*; recorded by Pemberton (1943) from rats, mice, and mongoose; recorded by Simmons et al. (1944) from rats and mice; recorded by Bonnet (1948) from rats in the Kula region. *ADDITIONAL RECORD*. Haleakala National Park (Crater Observatory), 2,989 m: 1 ♀, ex *R. rattus*, July 1962, R. J. Badaracco.

HAWAII. Recorded by Ewing (1924) from *M. musculus* and *R. norvegicus* in Honokaa; recorded by Pemberton (1925) from mice in the Hamakua Dist.; recorded by Eskey (1934) from rats in Ahualoa, Honokaa, Kalopa, Kukaiau, Kukuihaele, Lower Pohakea, and Upper Pohakea, and from *M. musculus* in Hamakua Dist. and vicinity of Hilo, and from rats in vicinity of Hilo, that is, Olaa (Keaau), and the S Hilo Dist.; recorded by Pemberton (1943) from rats, mice, and mongooses; recorded by Simmons et al. (1944) from rats and mice; recorded by Gross and Bonnet (1951) in the Hamakua Dist.; recorded by Kartman and Lonergan (1955) from nest of Hawaiian rat in Kaunamano Gulch, Hamakua Dist.; recorded by Gross (1961) from all rodent species in the Hamakua Dist.; recorded by Malley and Devick (1968) from *M. musculus* and other rodents; recorded by Haas (1969) from rodents near Kukuihaele. *ADDITIONAL RECORDS*. Halepiula, 1,769 m: many, ex *M. musculus*, Feb., Mar. 1964, G. P. Mills and T. Saguicio; 1 ♂, 2 ♀♀, ex *R. norvegicus*, Feb. 1964, GPM & TS; 3 ♀♀, ex *R. rattus*, Feb. 1964, GPM & TS. Halepohaku (cabins), 2,818 m: 2 ♂♂, 3 ♀♀, ex *M. musculus*, May 1969, P. Q. Tomich; (picnic area) 2,940 m: 1 ♂, 1 ♀; 1 ♂, 4 ♀♀, ex *M. musculus*, May 1969, PQT. Hanaipoe, 1,574 m: 5 ♀♀, ex *M. musculus*, Feb. 1964, GPM & TS; 2 ♂♂, ex *R. rattus*, Feb. 1964, GPM & TS. Hawaii Volcanoes National Park (Kipuka Nene), 915 m: 1 ♂, ex *R. rattus*, Dec. 1961, G. E. Haas; (Kipuka Puaulu (Bird Park)), 1,220 m: 1 ♂, 1 ♀, ex *R. rattus*, Mar. 1965, R. Y. W. Lee. Hawi (2.3 km SSW), 528 m: 1 ♂, 1 ♀; 1 ♂; 1 ♂, ex *M. musculus*, Jan., Feb. 1962, GEH & T. Ishinaga; 1 ♀, ex *R. exulans*, Jan. 1962, GEH & TI. Honokaa (3 km SW: Ahualoa Homesteads), 610 m: 3 ♀♀, ex *R. norvegicus* nest with rat, Apr. 1963, GPM & TS; (1.7 km NE), 168 m: 1 ♂, 3 ♀♀, ex *M. musculus* nest, Jan. 1964, S. Kaaekuahiwi & E. Auna. Kahawailiilii Gulch (N slope Mauna Kea), 1,598 m: 2 ♀♀, ex *R. rattus*, Feb. 1964, GPM & TS. Kapulena (2.8 km SW: Hamakua Forest Reserve), 610 m: 29 ♂♂, 15 ♀♀, ex *R. exulans* nest, Mar. 1964, W. Mills. Keanakolu (ranger station), 1,610 m: 3 ♂♂, 2 ♀♀, ex *M. musculus*, Mar. 1964, GPM & TS. Kilauea Military Camp (1.6 km NE), 1,225 m: 1 ♂, ex *R. rattus*, June 1962, W. Graf; 2 ♂♂, 2 ♀♀; 2 ♀♀, ex *M. musculus*, June, July 1962, WG. Kohala Mtn. (E slope Haloa), 964 m: many, ex *M. musculus*, Apr. 1964, GPM & TS. Kukaiau Ranch (NE slope Mauna Kea), 1,586 m: 5 ♂♂, 8 ♀♀, ex *R. norvegicus*, Mar. 1964, GPM & TS; 6 ♀♀, ex 2 *R. rattus*, Feb. 1964, GPM & TS; (Iolehaehae Camp), 1,915 m: 1 ♂, 2 ♀♀, ex *M. musculus*, Feb. 1964, GPM & TS; 3 ♀♀, ex *R. rattus*, Mar. 1964, GPM & TS. Kukuihaele, 259 m: 1 ♂, ex *Herpestes auropunctatus*, Aug. 1962, SK; 270 m: 23 ♂♂, 31 ♀♀, ex 6 *M. musculus* nests in subterranean nest boxes, Jan., Mar. 1961, GEH; (3 km SSW: Hamakua Forest Reserve), 564 m: many, ex many *M. musculus* & *R. exulans*, Mar.-Oct. 1961, GEH & C. M. Wheeler; many, ex *R. norvegicus*, Mar., Apr. 1961, GEH & CMW; many, ex many *R. rattus*, May-Sept. 1961, GEH & CMW. Makahalau Camp, 1,171 m: 2 ♂♂, 2 ♀♀, ex *M. musculus*, Nov. 1962, GEH & GPM; 1 ♂, 4 ♀♀, ex 2 *R. rattus*, Nov. 1962, GEH & GPM. Mana, 1,074 m: 2 ♂♂, 7 ♀♀, ex *R. rattus*, Nov. 1962, GEH & GPM. Napoopoo (1 km E), 76 m: 1 ♀, ex *M. musculus*, Feb. 1962, N. Wilson & SK. Paauilo (5.4 km SE), 640 m: 1 ♂, 1 ♀, ex *R. exulans* nest, Oct. 1963, WM. Palihooukapapa, 1,269 m: 4 ♂♂, 4 ♀♀, ex *R. rattus*, Nov. 1962, GEH & GPM. Pohakuloa, 1,983 m: 3 ♂♂, 9 ♀♀, ex 3 *M. musculus*, July 1962, WG. Puuanahulu, 665 m: many, ex many *M. musculus*, Sept. 1963, GEH & GPM. Puu Keanui cinder cone (N Kona Dist., Puu Lehua Quadrangle), 1,594 m: 13 ♂♂, 11 ♀♀, ex *M. musculus*, Jan. 1963, GEH. Puu Kihe (NE slope Mauna Kea, foresty plot),

2,349 m: 3 ♂♂, 5 ♀♀, ex 2 *M. musculus*, Mar. 1964, GPM & TS; (NE slope Mauna Kea, cabins), 2,364 m: 6 ♀♀, ex 4 *R. rattus*, July 1968, SK & EA. Puu Waawaa (ranch headquarters), 842 m: many, ex many *M. musculus*, Sept. 1963, GEH & GPM. Umikoa (Kukaiau Ranch Headquarters), 1,067 m: many, ex *M. musculus* & *R. norvegicus*, Feb. 1964, GPM & TS. Waikii (5.2 km SSE: Kilohana Girl Scout Camp), 1,708 m: 2 ♂♂, 2 ♀♀; 1 ♂, 3 ♀♀, ex *R. rattus*, Apr., Sept. 1964, R. I. Baldwin.

HOSTS. Recorded from bodies and nests of *M. musculus, R. exulans*, and *R. norvegicus*; from bodies of *H. auropunctatus* and *R. rattus*.

The mouse flea, *L. segnis*, was first recorded by Ewing (1924) from specimens collected in 1922-1923 in Honokaa by Pemberton. This species probably entered the Hawaiian Islands in the nineteenth century if not earlier, on *M. musculus, R. norvegicus*, and *R. rattus* that left ships calling at Hawaiian ports. Islands where this flea is most likely to be discovered are Molokai and Lanai.

L. segnis shows less aversion to heat than does *N. fasciatus*, but even so specimens are not often found near sea level. On the Island of Hawaii, mouse fleas are commonly encountered throughout the year on rodents trapped above 300 m. The maximum elevation from which specimens are recorded is 2,989 m, on Maui, but the host was trapped inside a building. Specimens were collected in a *M. musculus* subterranean nest as low as 168 m near Honokaa in January.

L. segnis ranges into high, dry areas such as Pohakuloa and Waikii (Kilohana Girl Scout Camp), on Hawaii, where the approximate average annual rainfall is between 381 and 508 mm. It also ranges into wet areas such as Paauilo, where the average rainfall amounts to more than 2,540 mm. Eskey (1934) recorded a light infestation in Olaa, where an average of 3,683 mm of rain falls per year.

Seasonal occurrence in rodent nests is unknown for lack of sufficient data, but for trapped rats Eskey (1934) made the general statement that at the highest altitudes from where his data were collected, *L. segnis* was most prevalent during "late spring," and below 1,500 feet (457 m) the greatest numbers were found during the "late winter months." For trapped mice he reported that the least infestation was during August and September. On the whole, our data from mice trapped in two localities in the Hamakua District more closely approach his statement regarding the time of maximum indices. In a *Eucalyptus* plantation 3 km SSW of Kukuihaele, 564 m, where we have data for March-October 1961, the mean number of mouse fleas on *M. musculus* was highest during June-August with a maximum of 14.0 (40% males). For *R. exulans* the flea index was highest during May at 2.7. In cane field 101b at Kukuihaele, 270-299 m, for which we have data for October 1959 through April 1961, the index for *M. musculus* was highest during January-May 1960 with a maximum of 1.9 (29% males) during February. For *R. exulans* the index was highest during April-July 1960 with a maximum of 0.3 in May.

The true host of *L. segnis* is *M. musculus*. Secondary hosts, which may be true hosts in some localities, are *R. norvegicus* and *R. rattus*.

Eskey (1934) pooled species of rats in each locality. For example, on Hawaii he trapped *R. exulans, R. norvegicus*, and *R. rattus*, so it is impossible to know if all three species were infested in all localities. In central Maui, however, he reported that *R. norvegicus* was absent from the lowlands, and only sparsely present in the upland Kula zone. He was first to record *L. segnis* from mongooses, but did not specify whether they were from Maui, Hawaii, or both islands.

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APPENDIX

A. Names of hosts

Branta sandvicensis (Vigors)	Hawaiian goose, nene
Diomedea immutabilis Rothschild	Laysan albatross
Gallus gallus (Linnaeus)	chicken
Lophortyx californicus (Shaw)	California quail
Passer domesticus (Linnaeus)	house sparrow, English sparrow
Puffinus pacificus (Gmelin)	wedge-tailed shearwater
Puffinus tenuirostris (Temminck)	short-tailed shearwater
Bos taurus Linnaeus	cattle
Canis familiaris Linnaeus	dog
Felis catus Linnaeus	cat
Herpestes auropunctatus (Hodgson)	small Indian mongoose
Homo sapiens Linnaeus	man
Leporillus conditor (Sturt)	stick-nest rat
Mus musculus Linnaeus	house mouse
Oryctolagus cuniculus (Linnaeus)	European rabbit
Rattus exulans (Peale)	Hawaiian rat, Polynesian rat
Rattus norvegicus (Berkenhout)	Norway rat, brown rat
Rattus rattus (Linnaeus)	roof rat, black rat
Rattus tunneyi (Thomas)	Tunney's rat
Sus scrofa Linnaeus	pig

B. Host synonymy

Felis domestica Erxleben	= *F. catus*
Herpestes birmanicus Thomas	= *H. auropunctatus*
Leporillus jonesi Thomas	= *L. conditor*
Rattus alexandrinus (Desmarest)	= *R. rattus*
Rattus culmorum (Thomas & Dollman)	= *R. tunneyi*
Rattus [exulans] hawaiiensis	= *R. exulans*
Rattus hawaiiensis Stone	= *R. exulans*

Rattus norvegicus may have included *R. exulans* before 1932.

SOURCES OF FIGURES

(Drawings, other than originals, modified to various degrees)

Originals: Figs. 1, 23-25, 27-34.

Sakaguti and Jameson, 1962: Figs. 6, 11, 15.

Smit, in Hopkins and Rothschild, 1953: Figs. 21, 26.

Smit, in Pollitzer, 1954: Figs. 2-5, 7, 8, 12-14, 16-20, 22, 35-40.

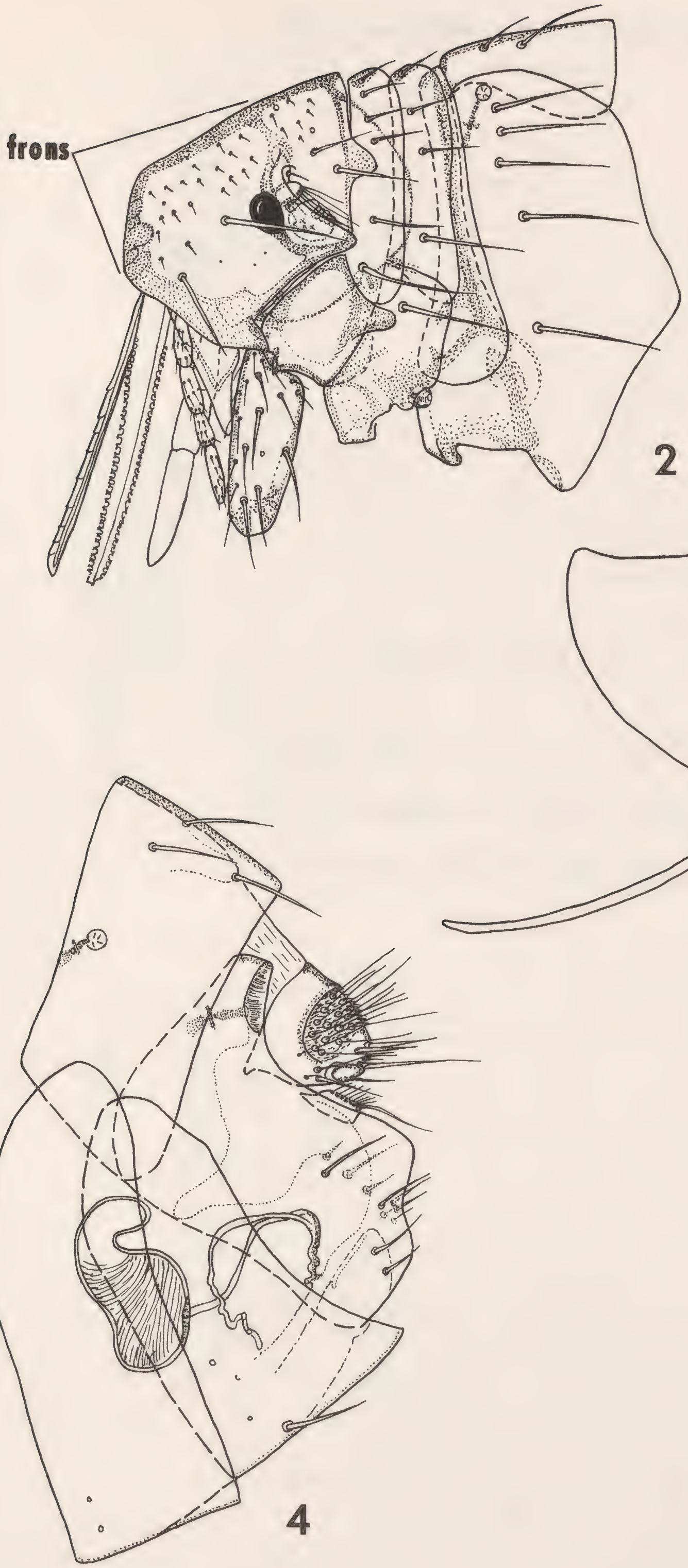
Smit, 1958: Figs. 9, 10.

Echidnophaga gallinacea (Westwood)

Fig. 2. Head, thorax, tergum I, and fore coxa, ♀

Fig. 3. Modified abdominal segment IX, ♂

Fig. 4. Terminal segments and genitalia, ♀



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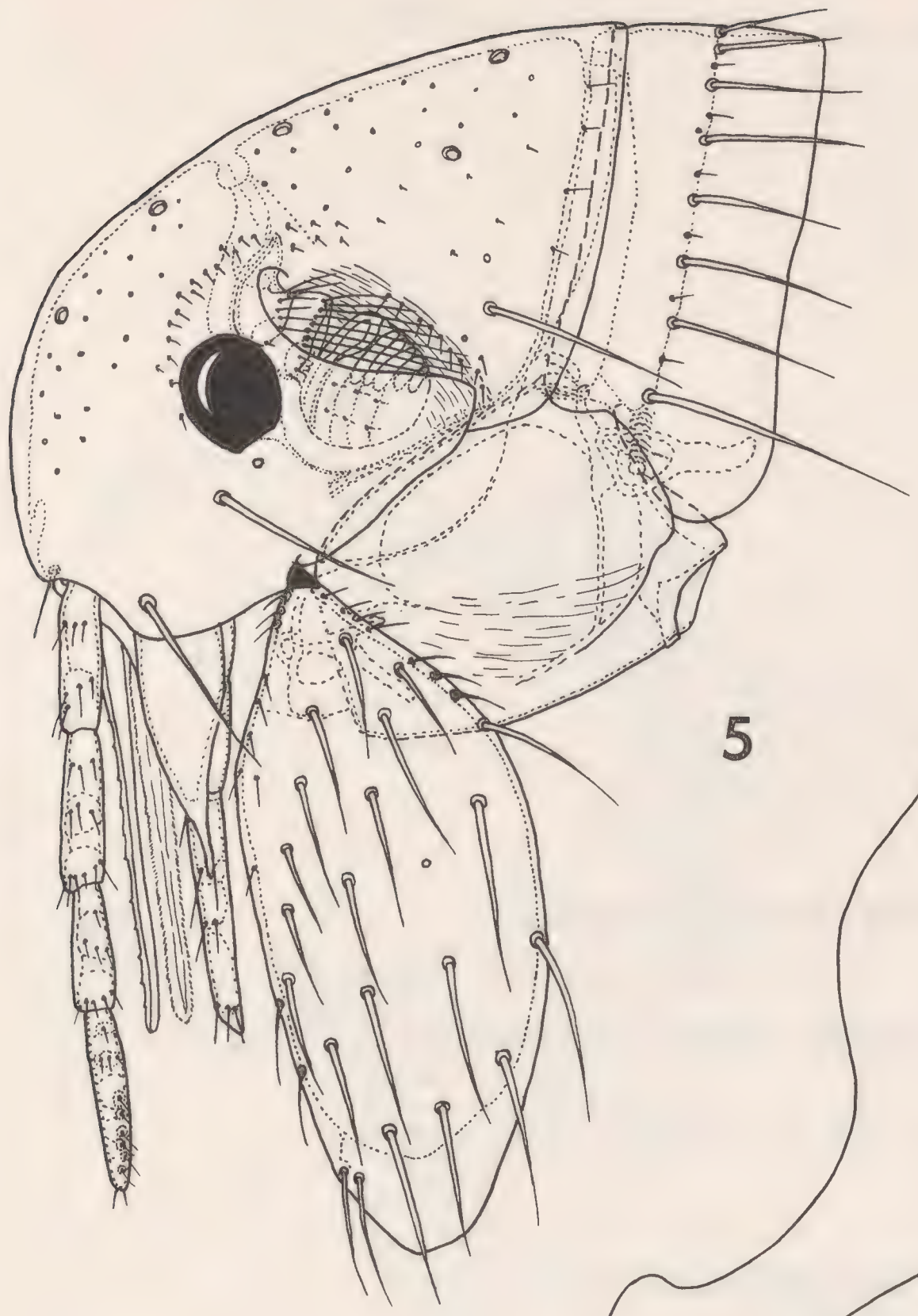
Pulex irritans Linnaeus

Fig. 5. Head, prothorax, and fore coxa, ♂

Fig. 6. Meso- and metathorax, ♂

Fig. 7. Modified abdominal segment IX, ♂



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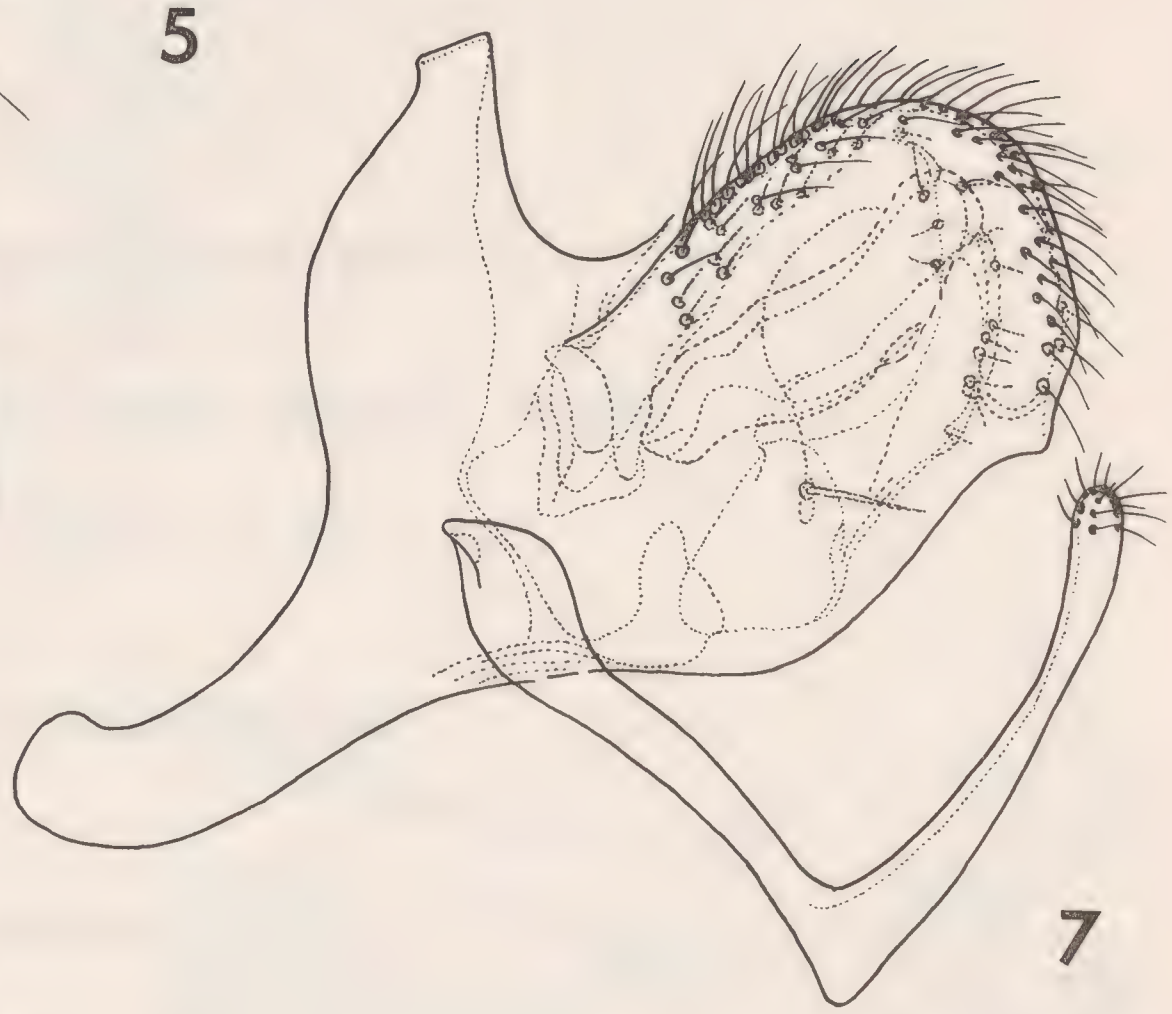

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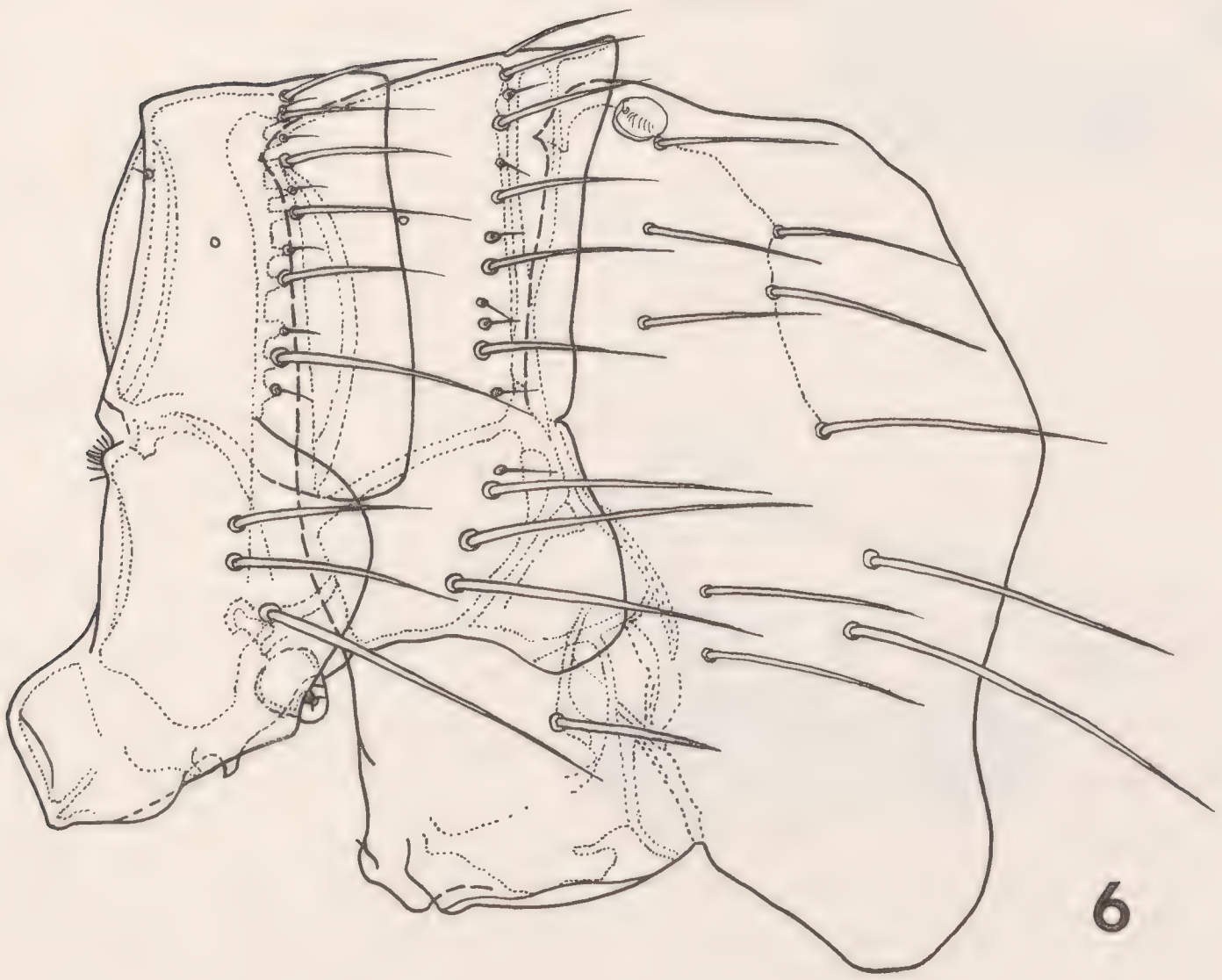

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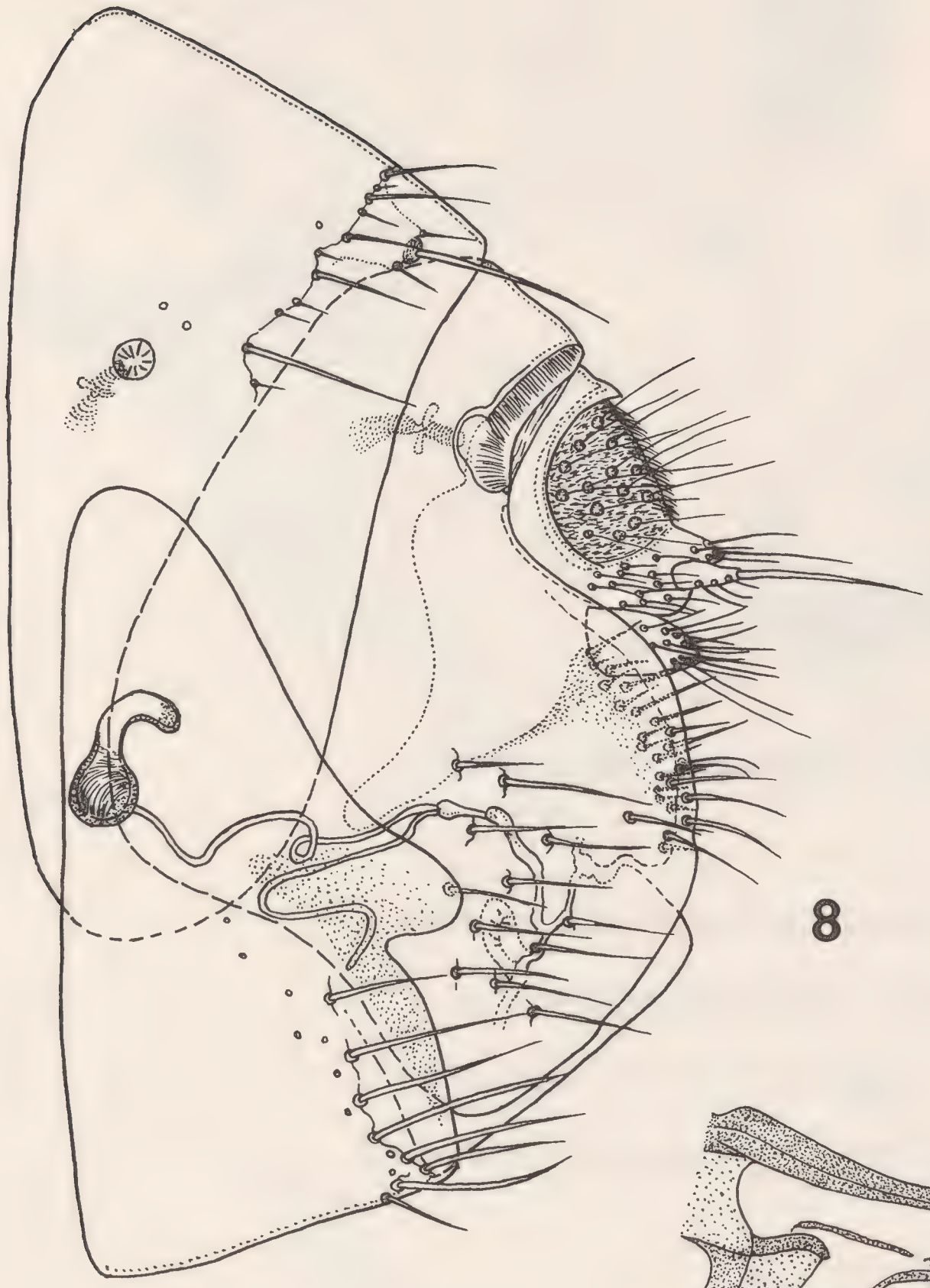
Pulex irritans Linnaeus

Fig. 8. Terminal segments and genitalia, ♀

Fig. 9. Aedeagus

Pulex simulans Baker

Fig. 10. Aedeagus



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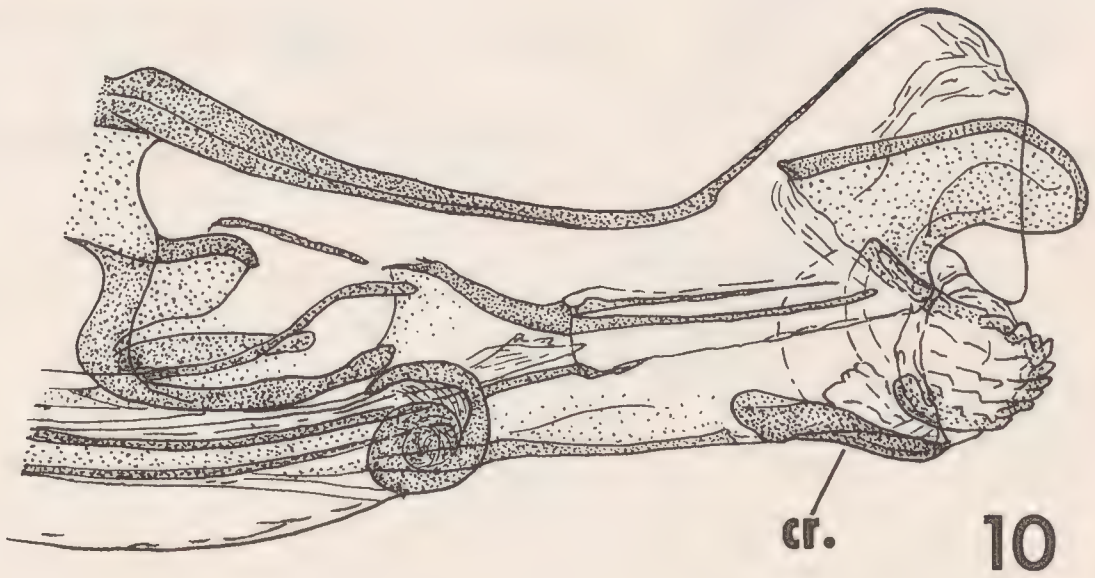

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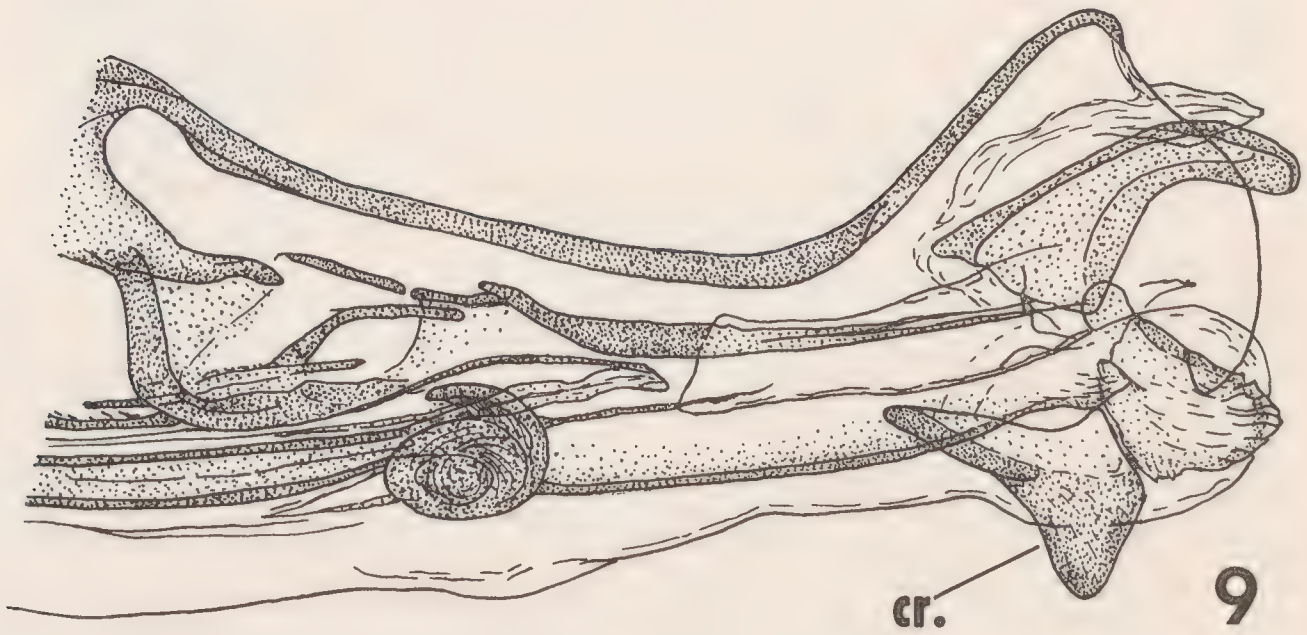

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Ctenocephalides felis felis (Bouché)

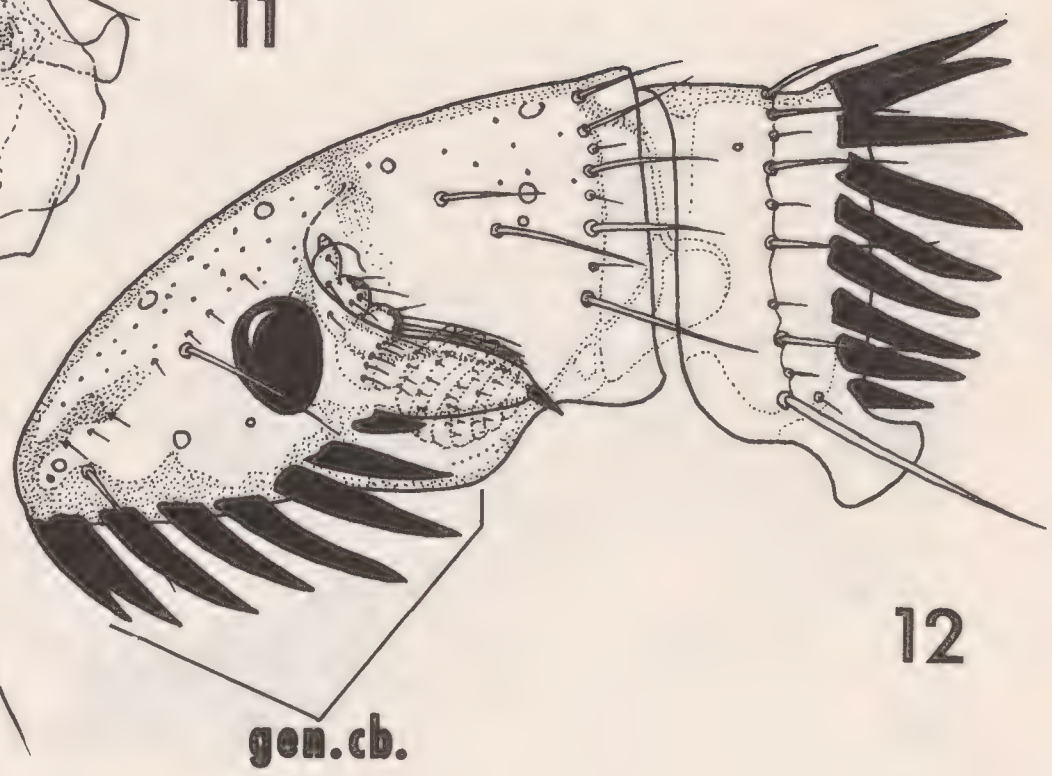
Fig. 11. Head, prothorax, and fore coxa, ♂

Fig. 12. Head and pronotum, ♀

Fig. 13. Modified abdominal segment IX, ♂

Fig. 14. Terminal segments and genitalia, ♀

11



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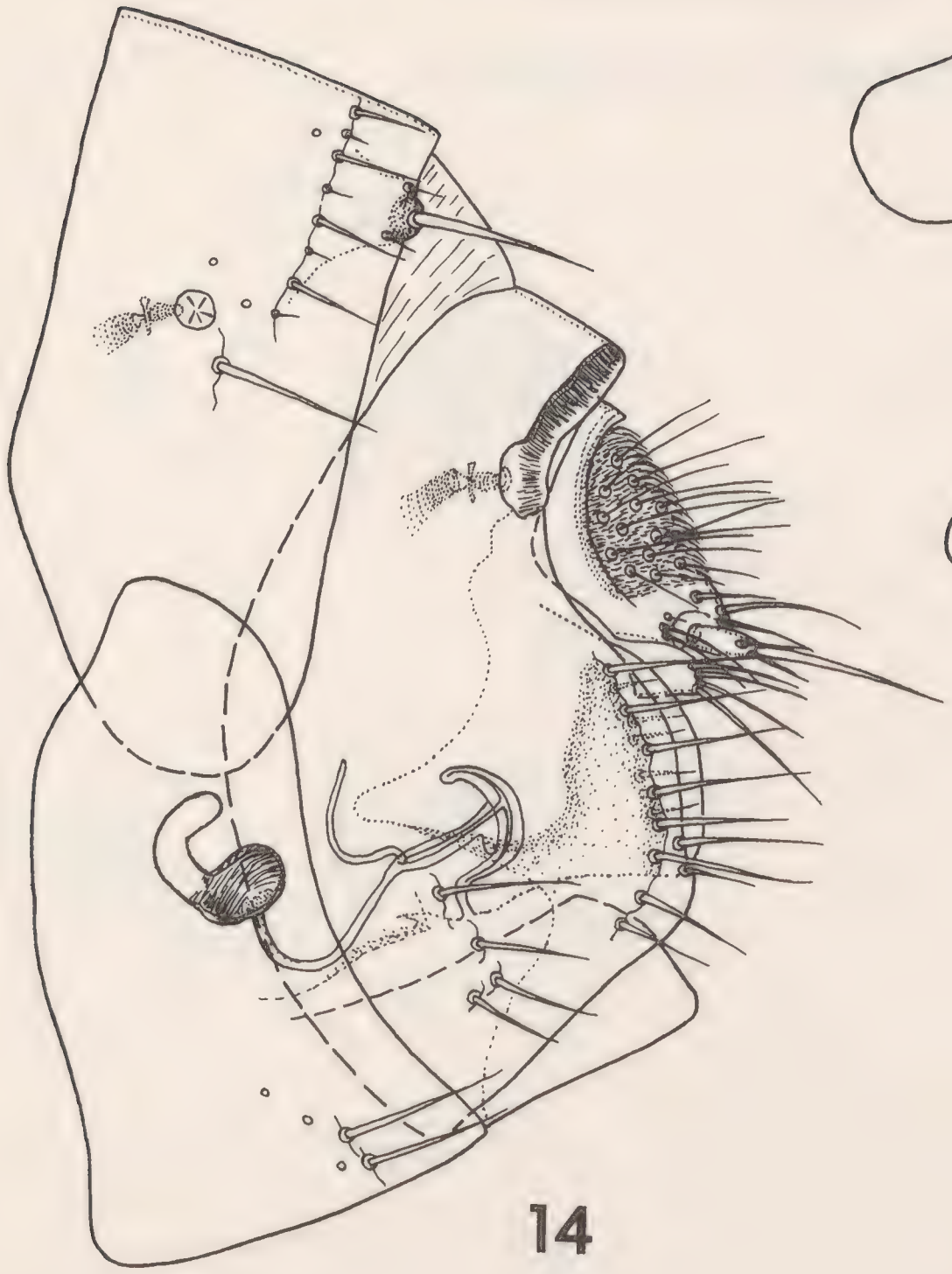

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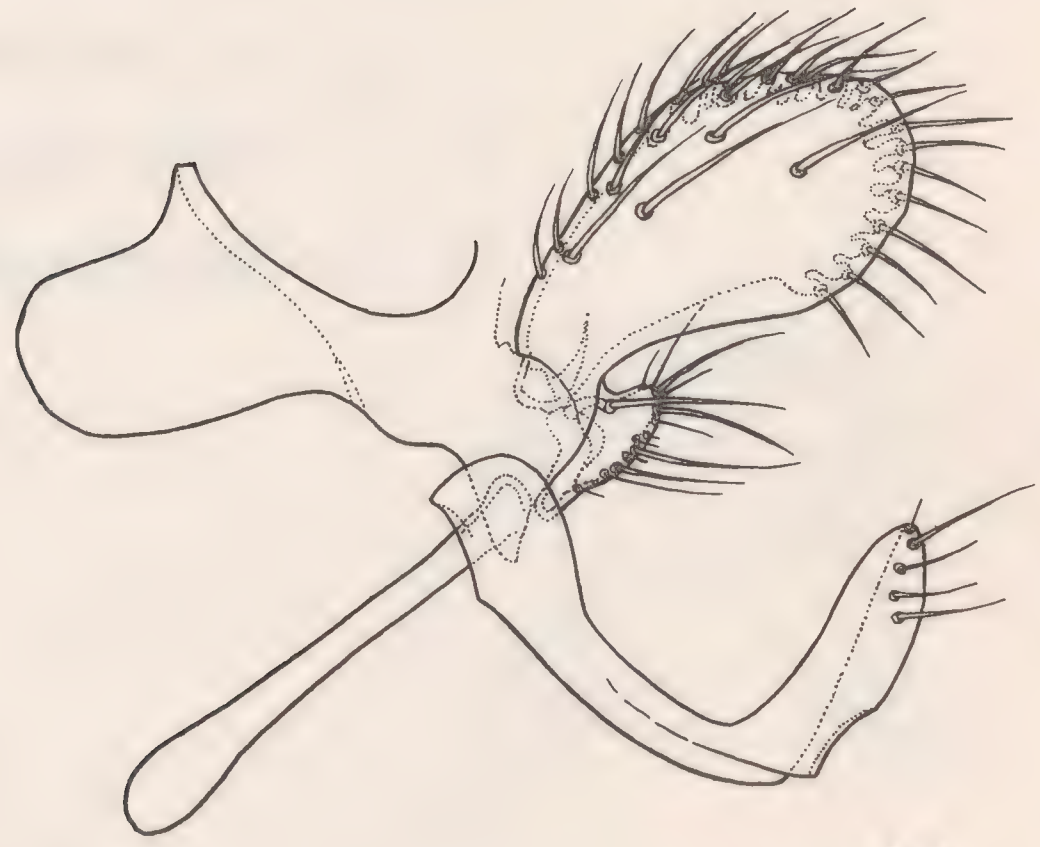

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Ctenocephalides canis (Curtis)

Fig. 15. Head, prothorax, and fore coxa, ♂

Fig. 16. Head and pronotum, ♀

Fig. 17. Modified abdominal segment IX, ♂

Fig. 18. Terminal segments and genitalia, ♀

15

16

gen.cb.

17

18

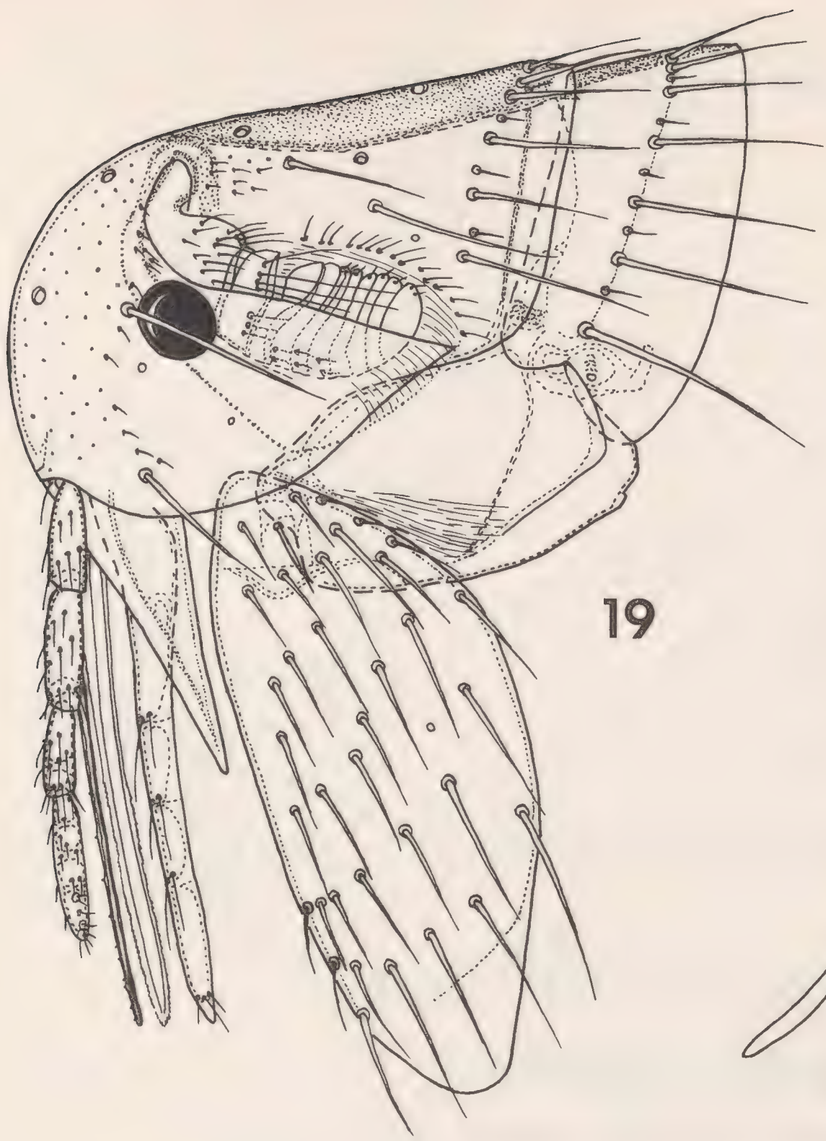
Xenopsylla cheopis (Rothschild)

Fig. 19. Head, prothorax, and fore coxa, ♂

Fig. 20. Modified abdominal segment IX, ♂

Fig. 21. Aedeagal apodeme

Fig. 22. Terminal segments and genitalia, ♀



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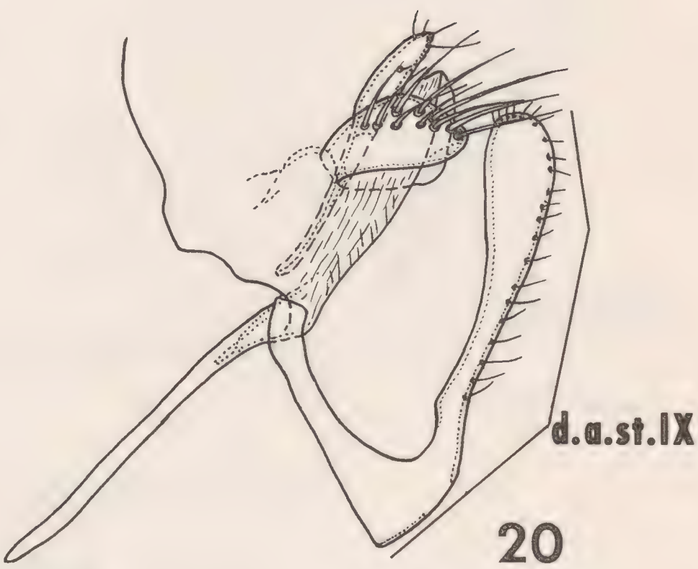

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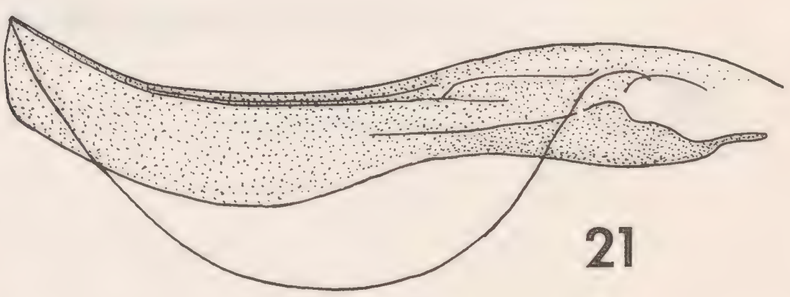

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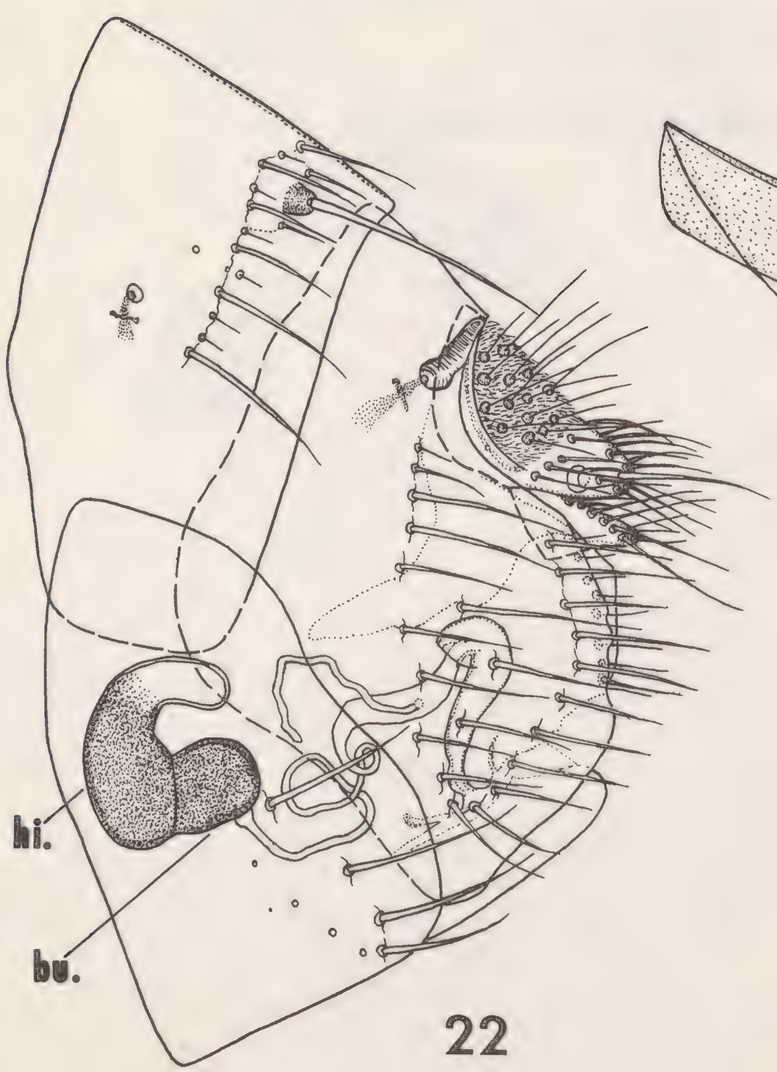


22

Xenopsylla vexabilis Jordan

Fig. 23. Head, prothorax, and fore coxa, ♀

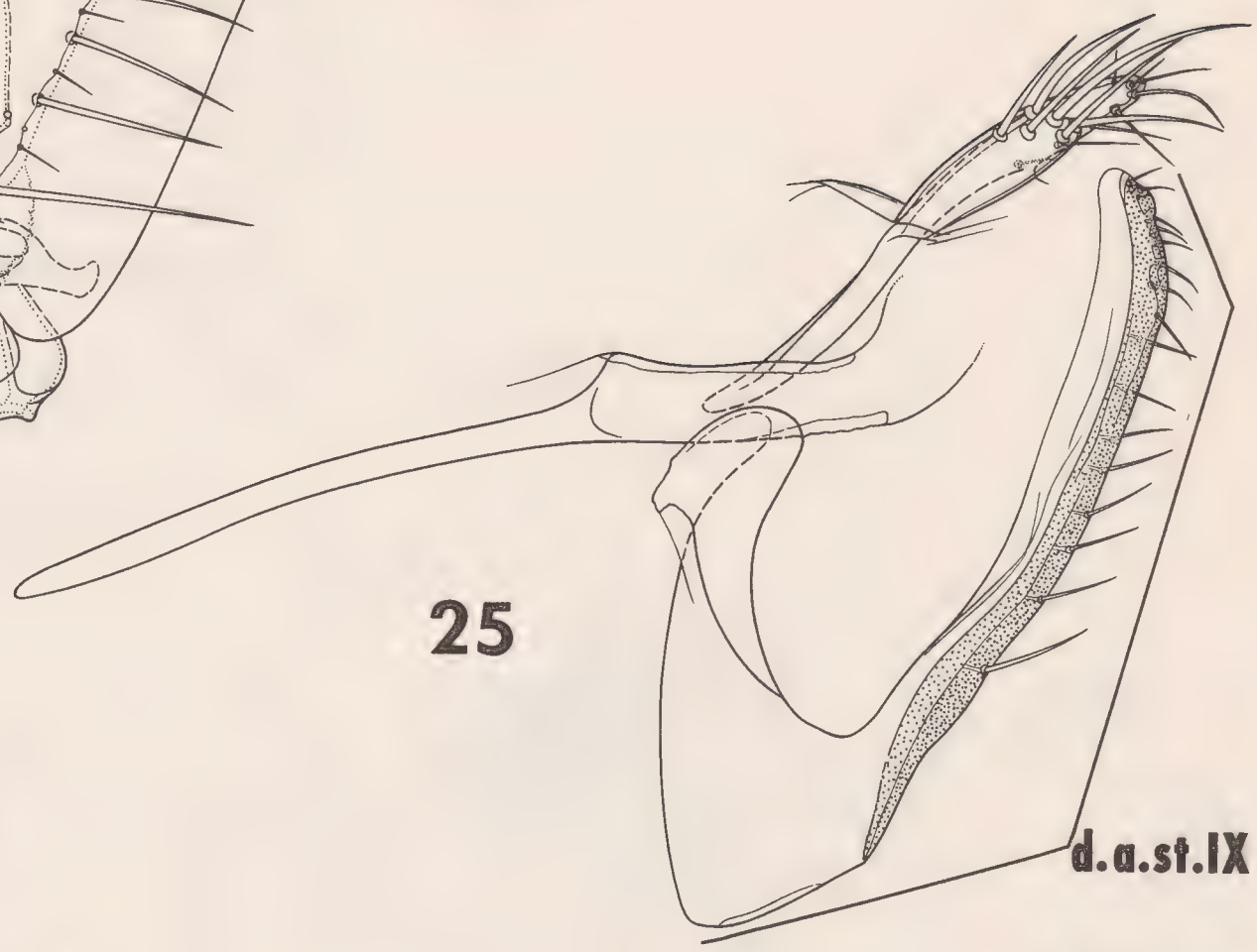
Fig. 24. Meso- and metathorax, ♀

Fig. 25. Modified abdominal segment IX, ♂

Fig. 26. Aedeagal apodeme

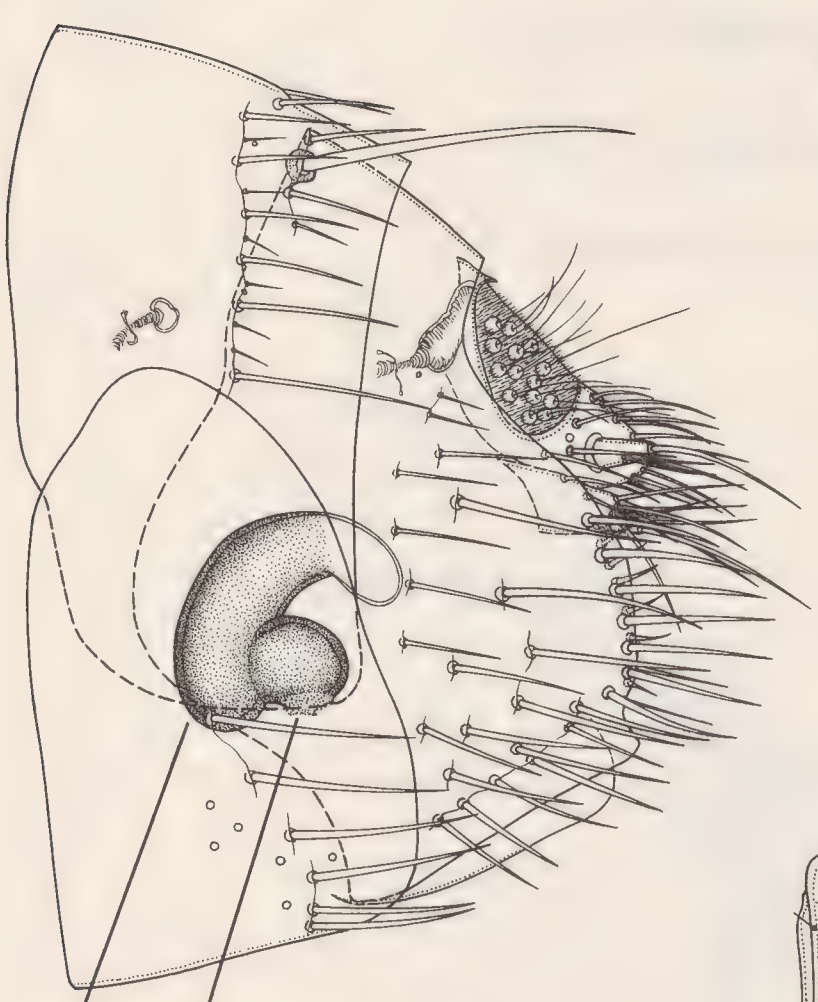
Fig. 27. Terminal segments and genitalia, ♀

23

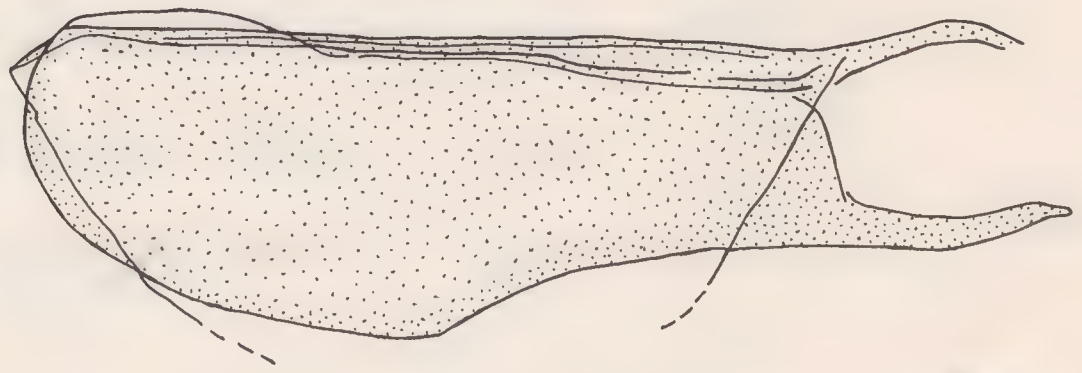


25

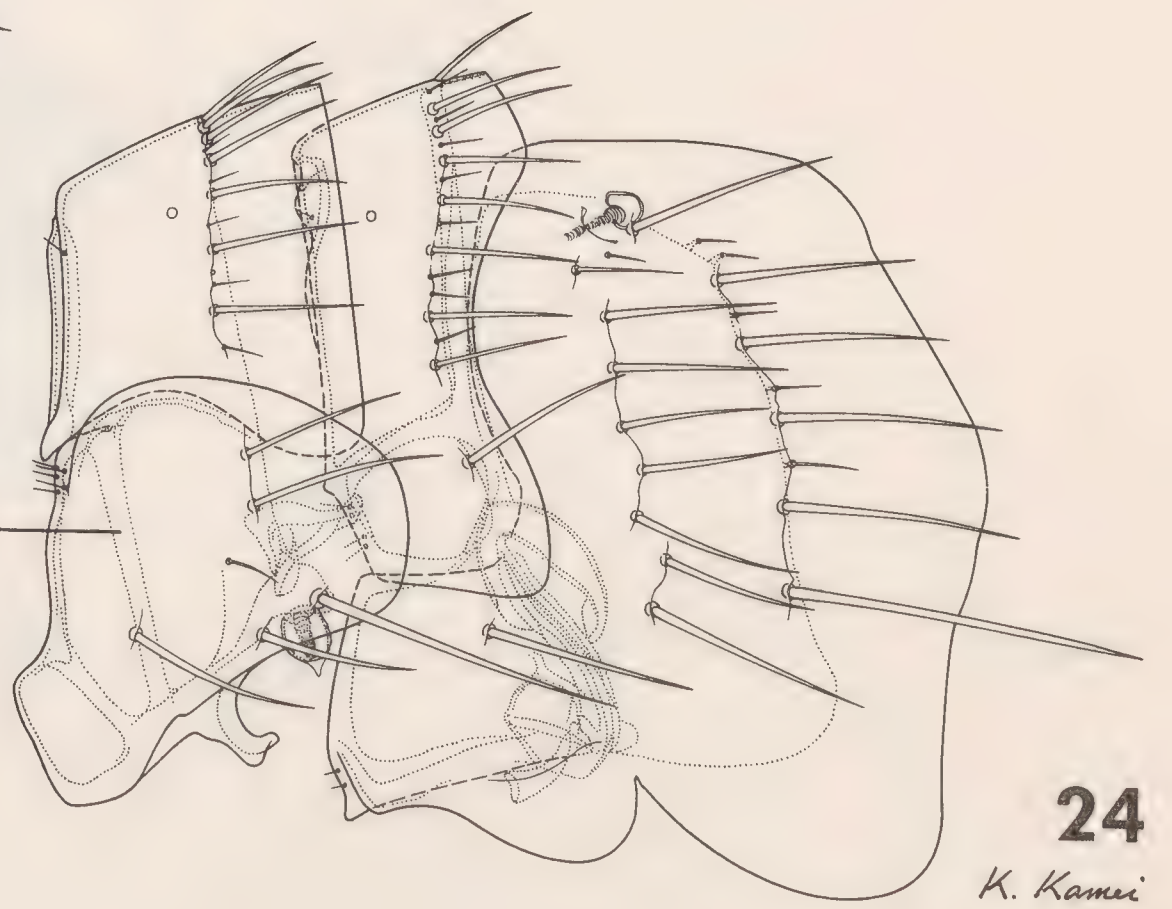
K. Kamei



27



26



24

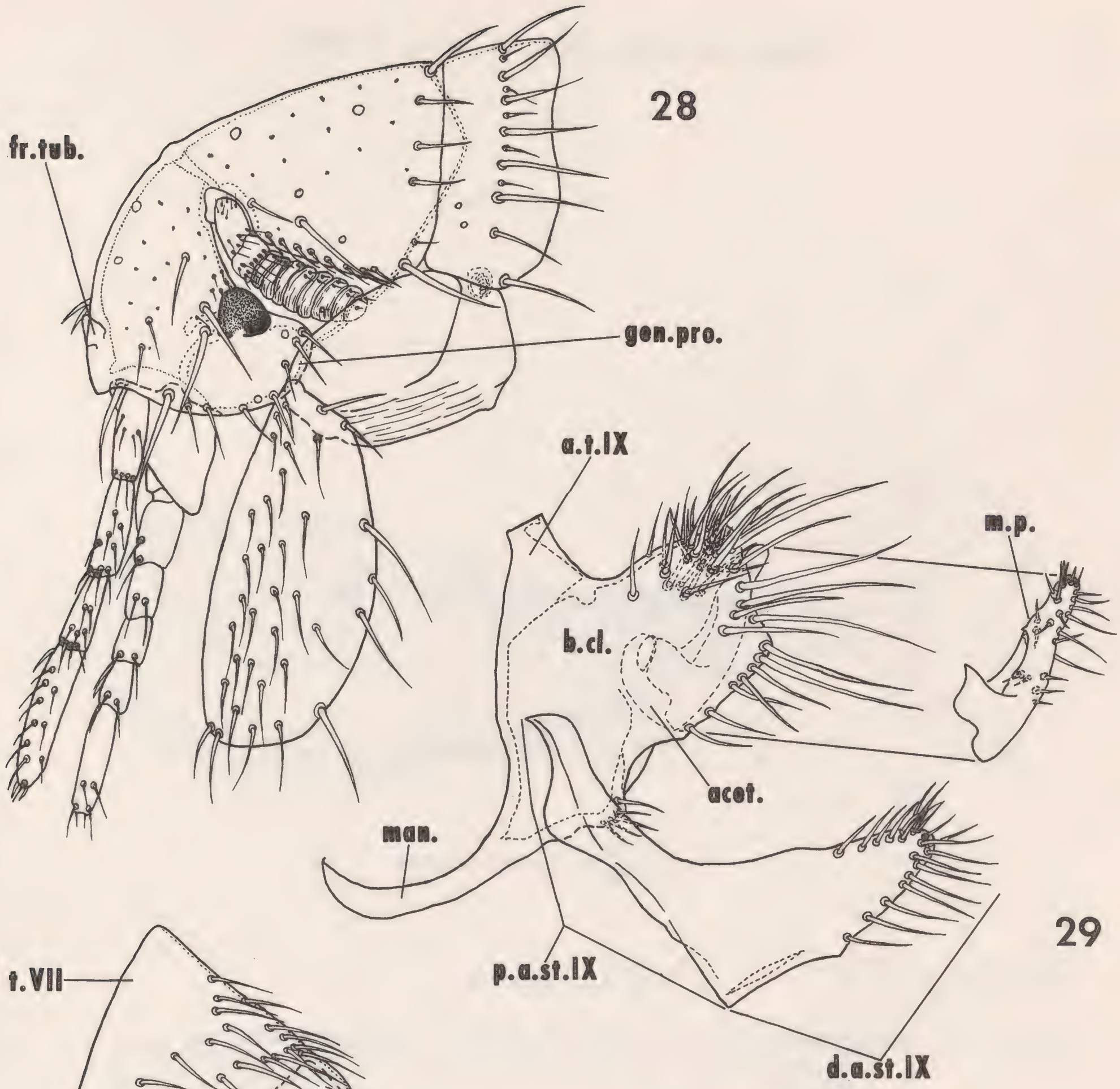
K. Kamei

Parapsyllus laysanensis Wilson, n. sp.

Fig. 28. Head, prothorax, and fore coxa, ♀

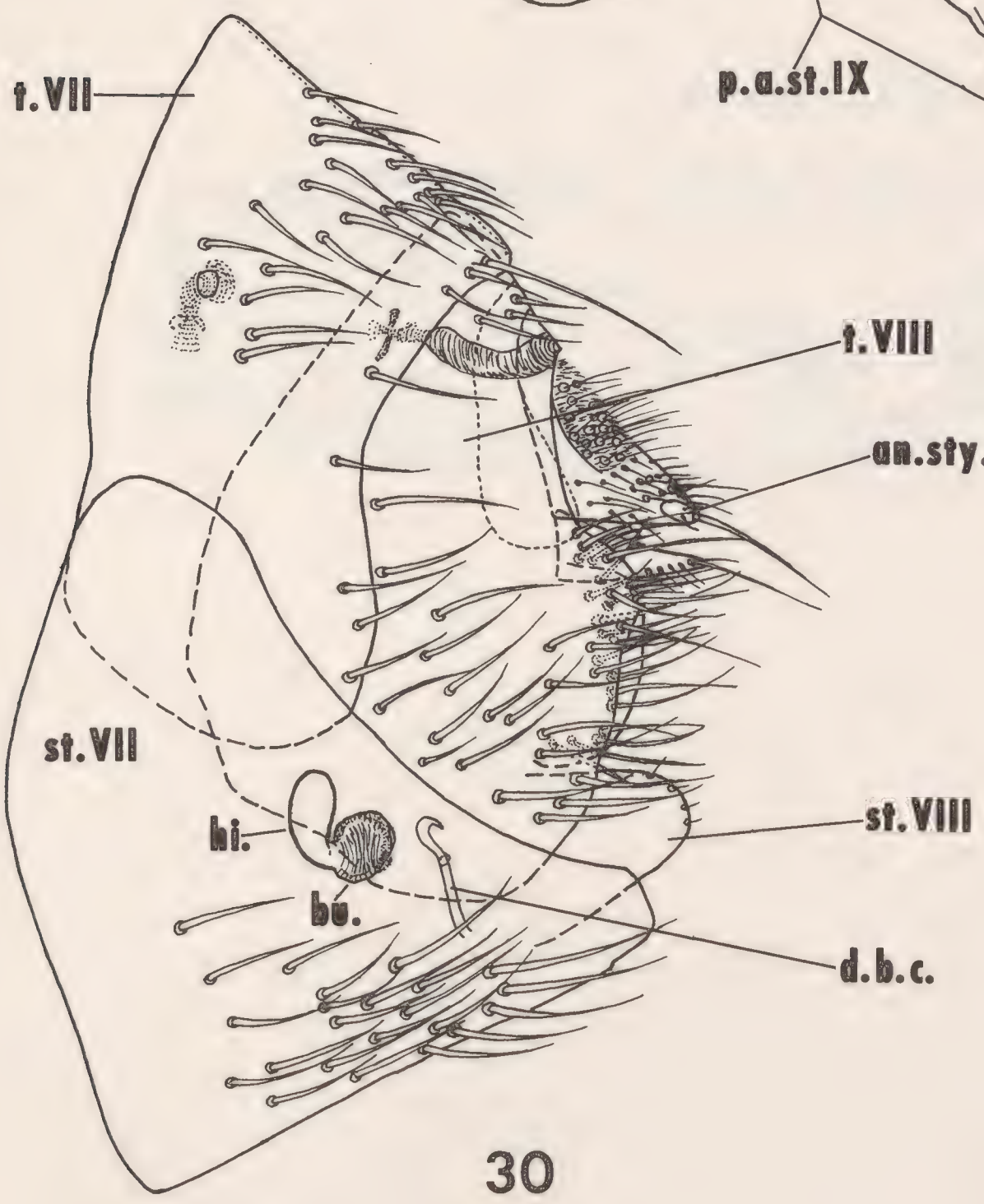
Fig. 29. Modified abdominal segment IX, ♂

Fig. 30. Terminal segments and genitalia, ♀


fr.tub.
gen.pro.
a.t.IX
m.p.
b.cl.
acot.
man.
p.a.st.IX
d.a.st.IX

28

29


t.VII
t.VIII
an.sty.
st.VII
hi.
bu.
st.VIII
d.b.c.

30

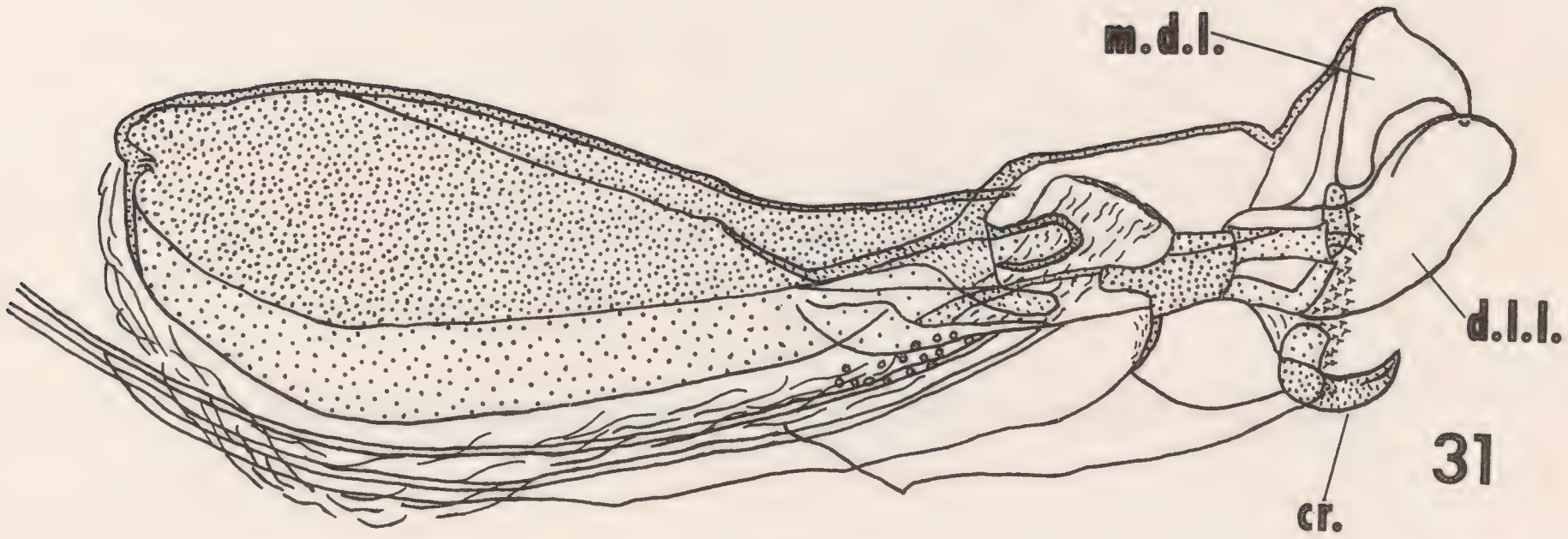
Parapsyllus laysanensis Wilson, n. sp.

Fig. 31. Aedeagus

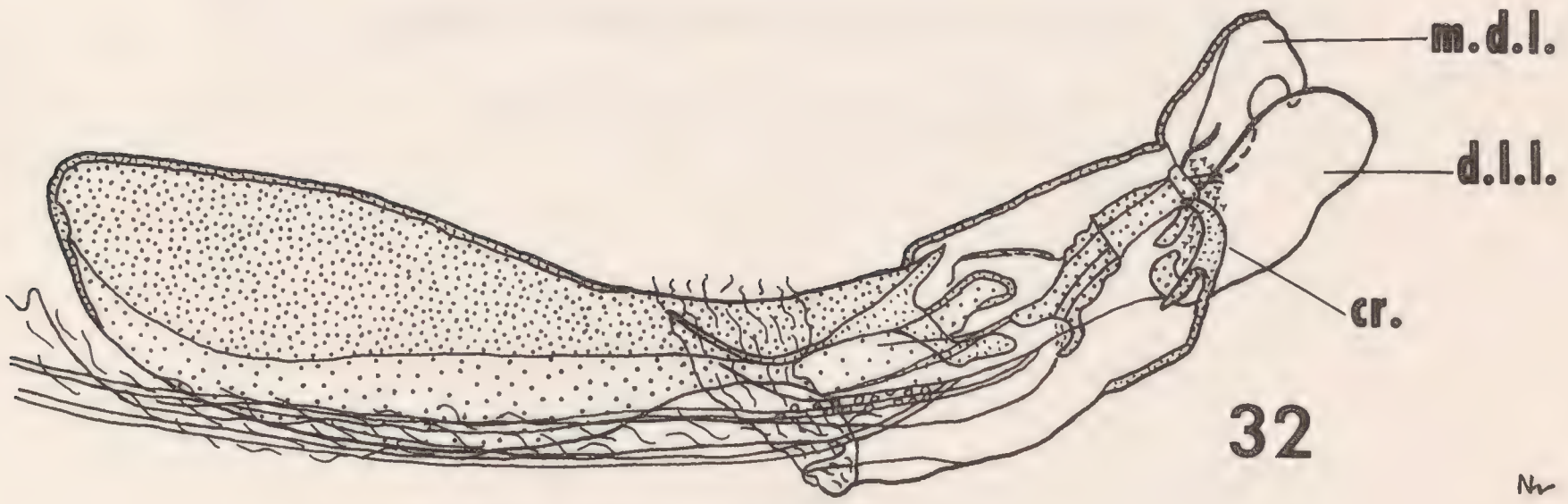
Parapsyllus taylori Jordan

Fig. 32. Aedeagus

Specimen from Furneaux Island, Tasmania, ex *Puffinus tenuirostris*, Nov. 1912, R. N. Atkinson (Brit. Mus. 1923.615).



31



32

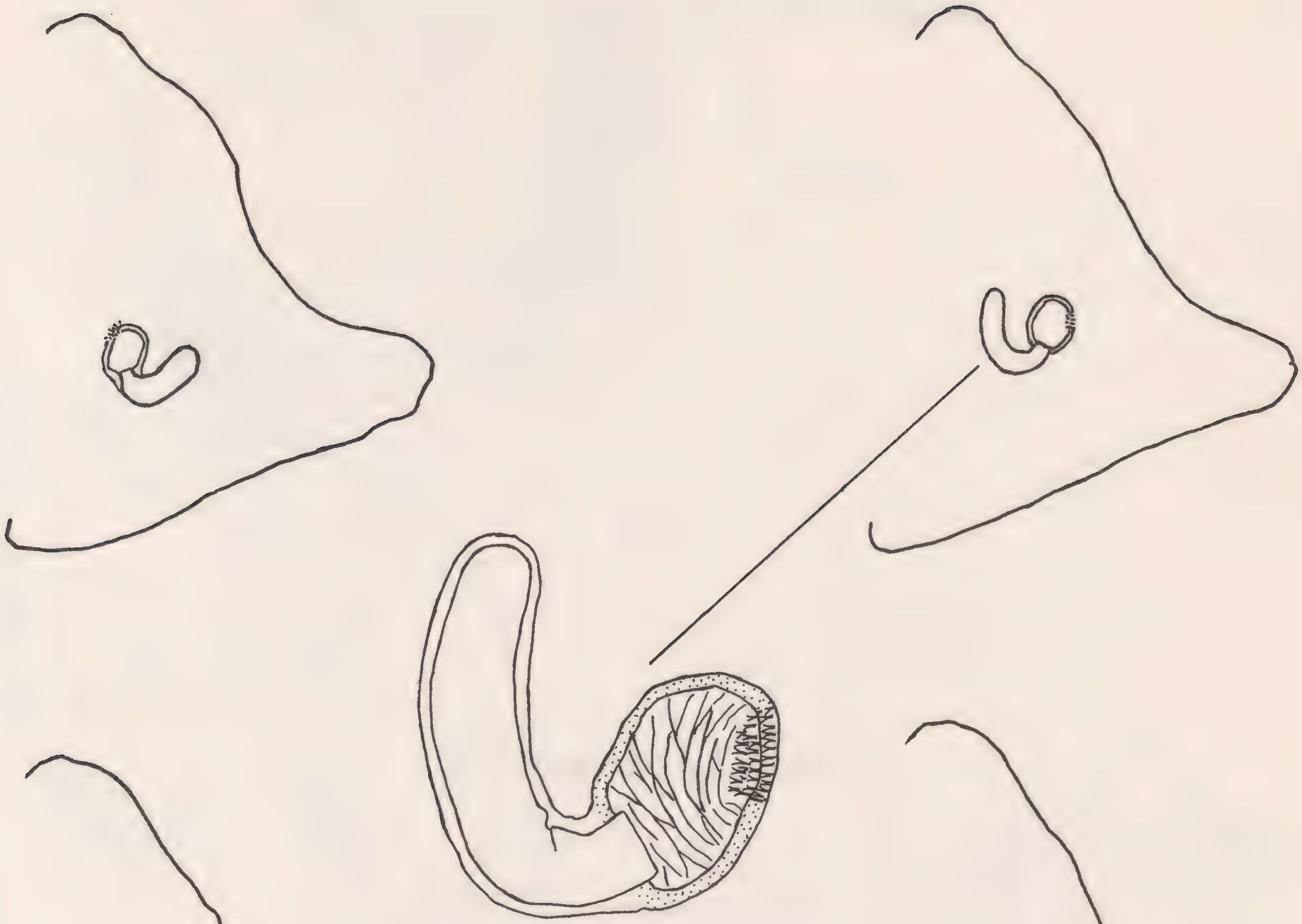
Parapsyllus laysanensis Wilson, n. sp.

Fig. 33. Sternum VII and spermatheca showing variation

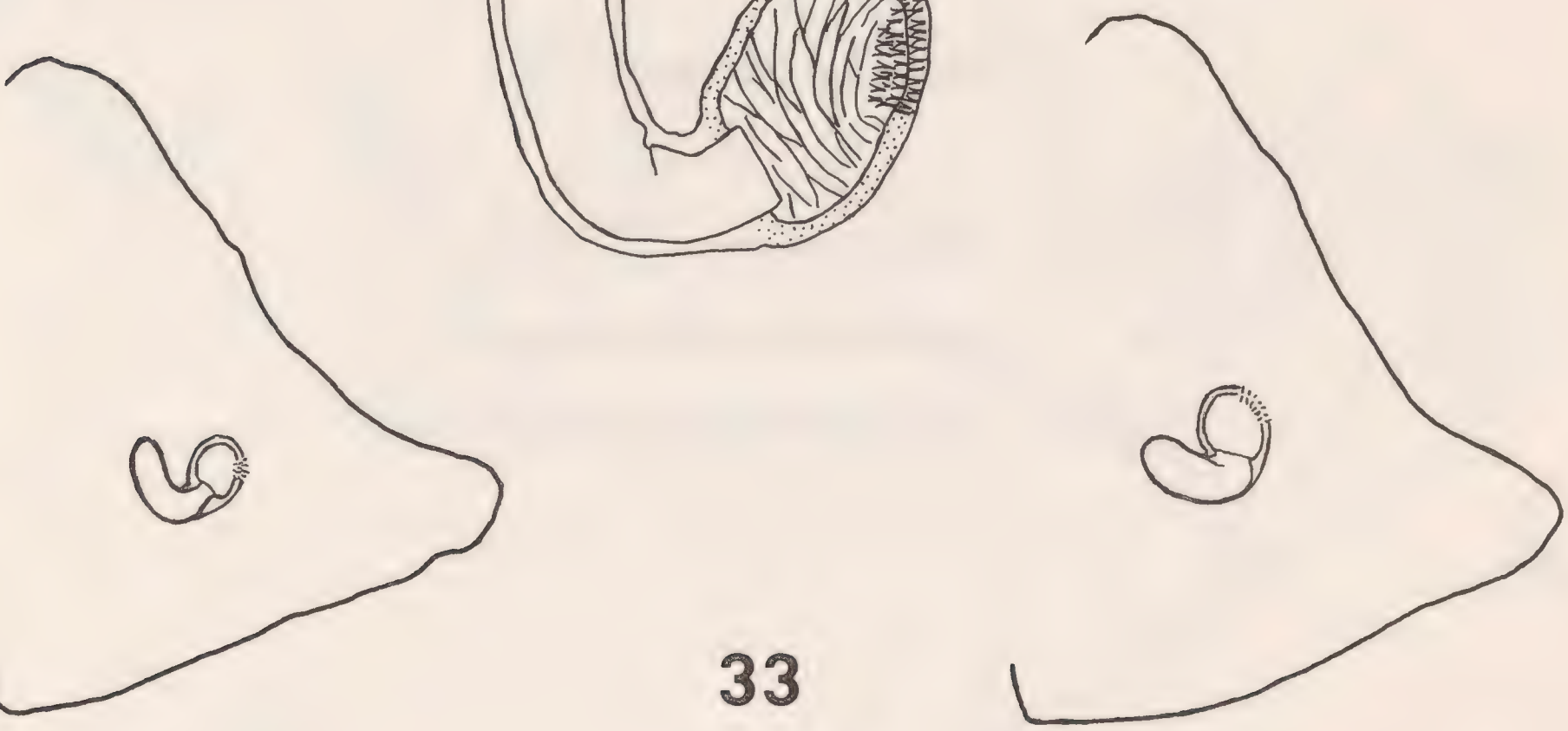
Parapsyllus taylori Jordan

Fig. 34. Sternum VII and spermatheca showing variation

Specimens with same data as Fig. 32.



33



34

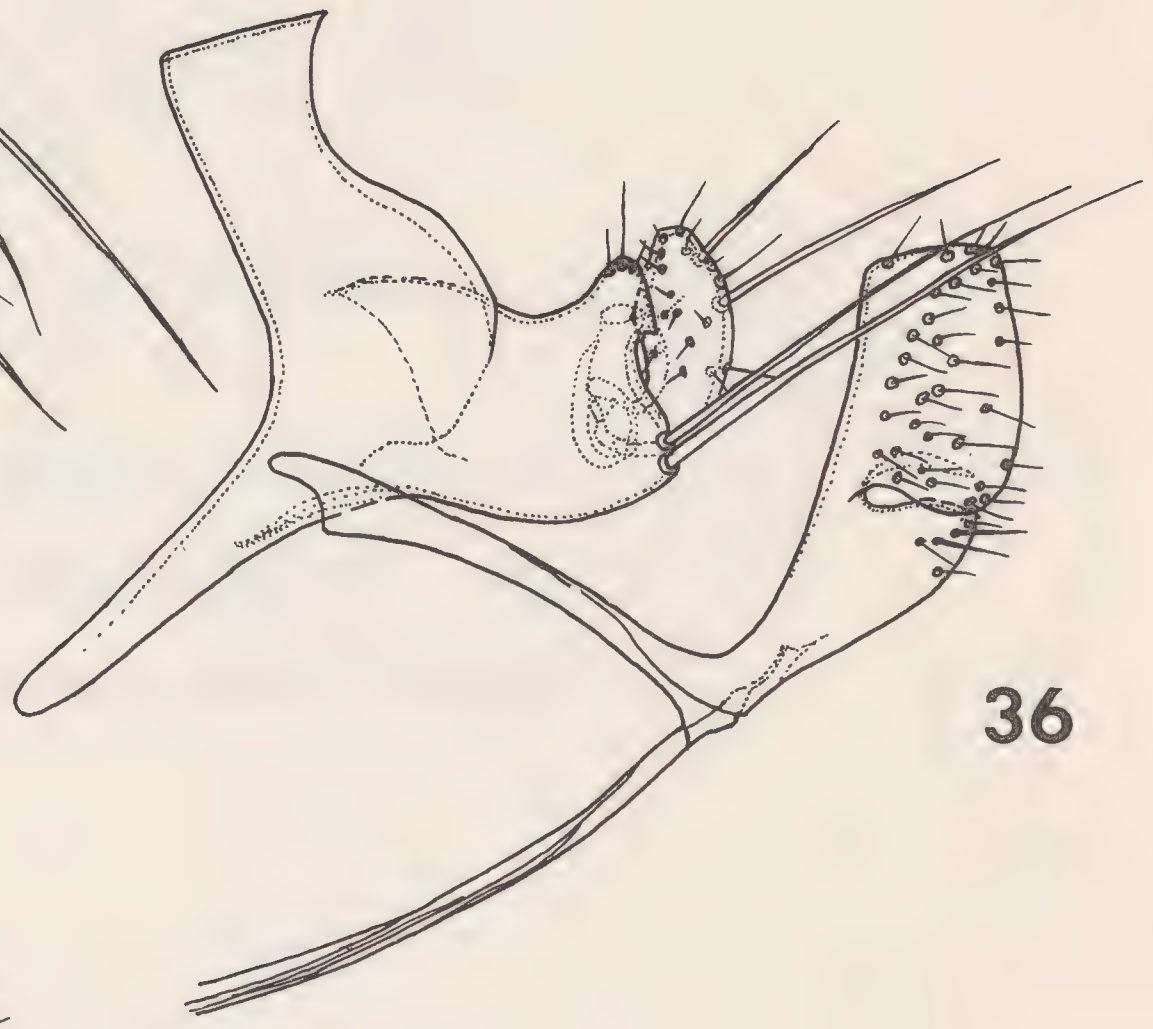
Nosopsyllus fasciatus (Bosc)

Fig. 35. Head, prothorax, and fore coxa, ♂

Fig. 36. Modified abdominal segment IX, ♂

Fig. 37. Terminal segments and genitalia, ♀

35



36

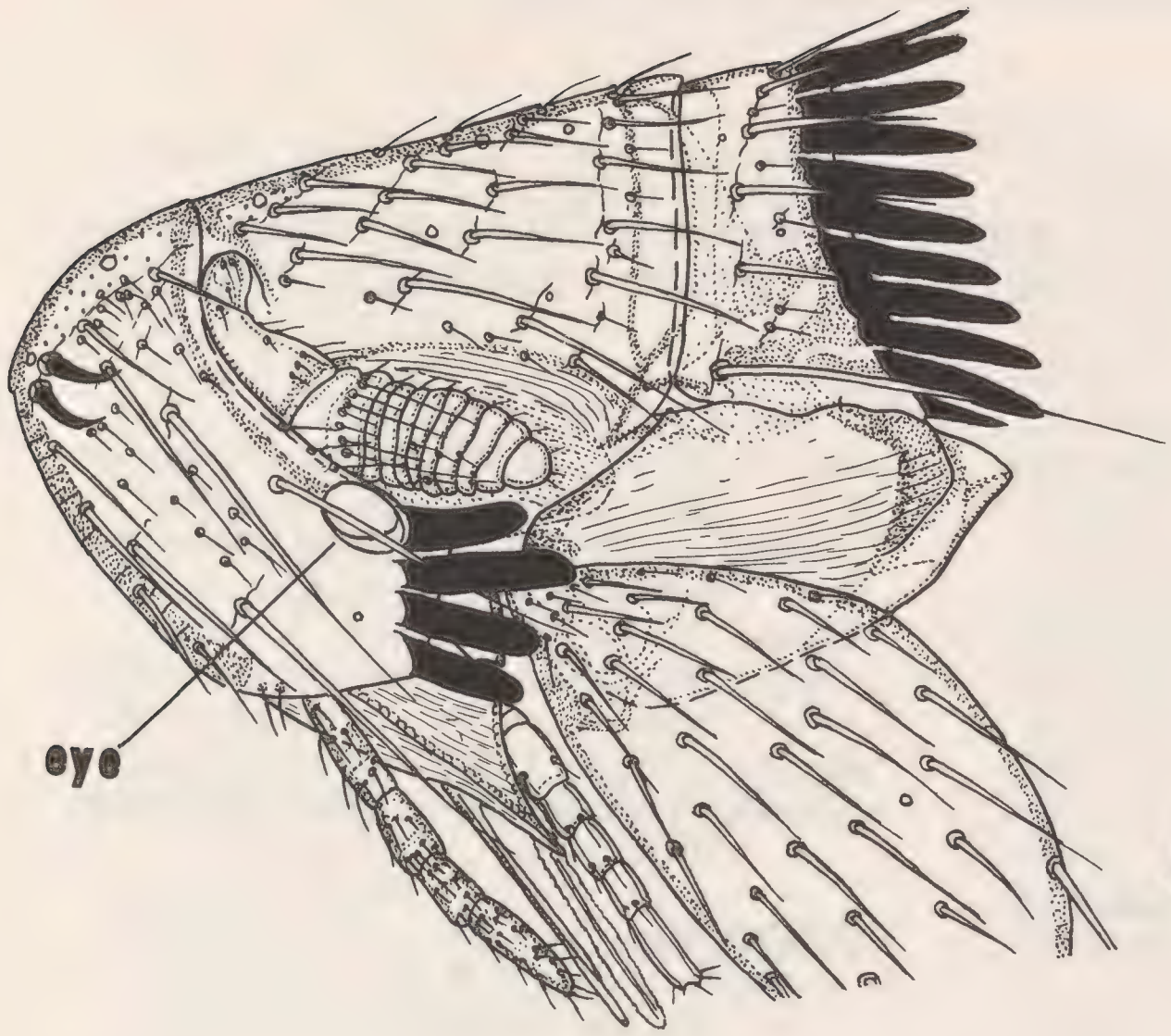
37

Leptopsylla segnis (Schönherr)

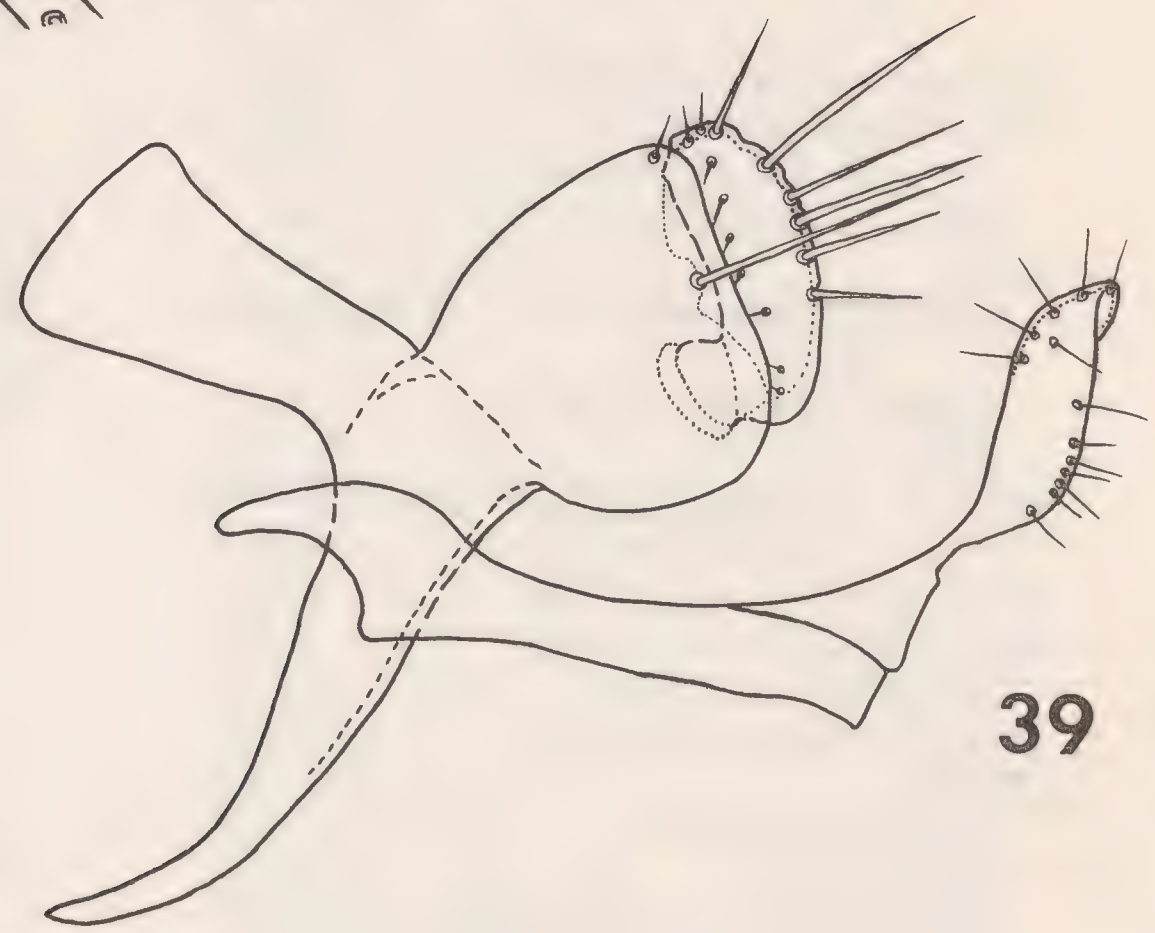
Fig. 38. Head, prothorax, and fore coxa, ♂

Fig. 39. Modified abdominal segment IX, ♂

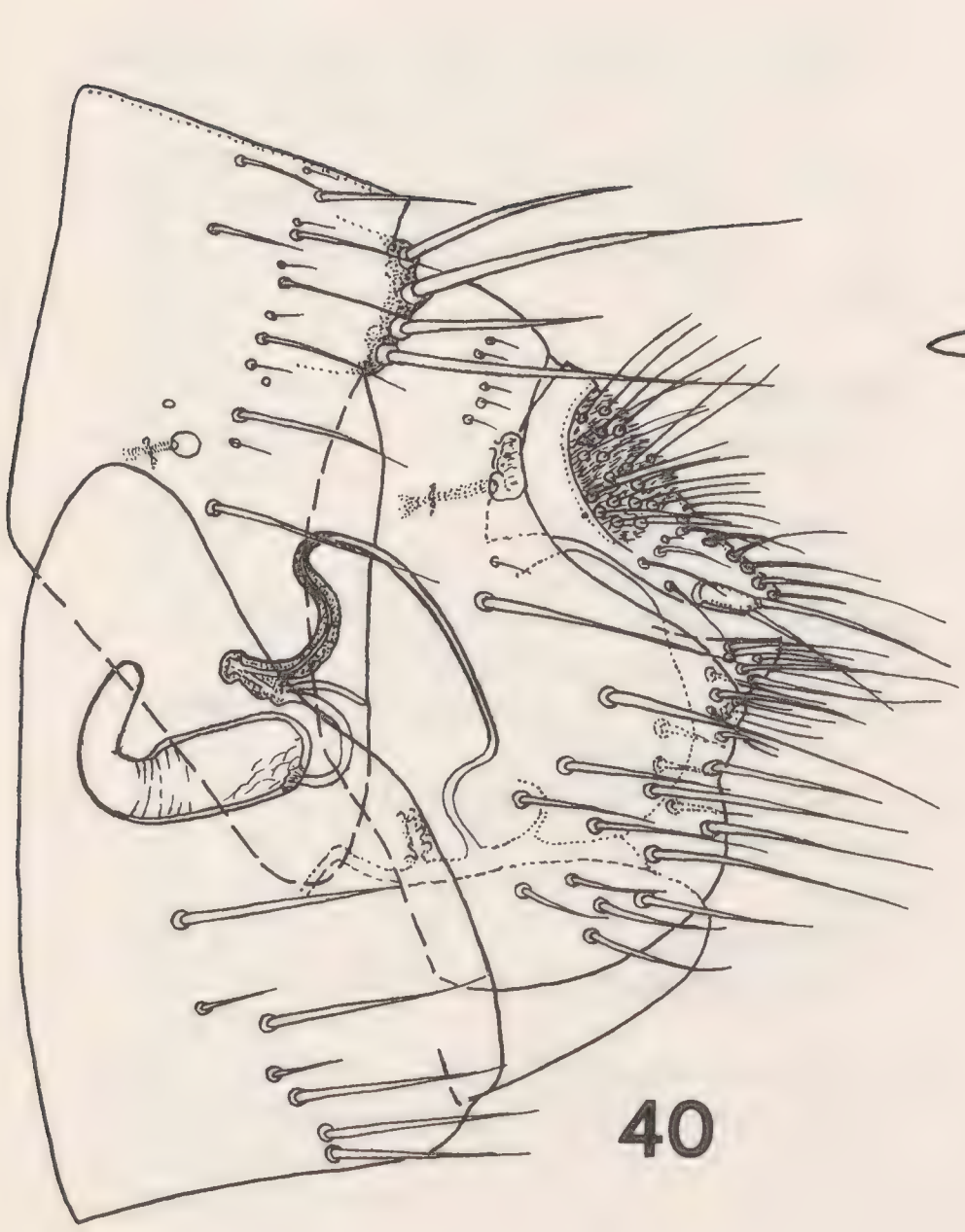
Fig. 40. Terminal segments and genitalia, ♀



38



39



40

INDEX

Valid scientific names are in roman type; synonyms and former combinations are in italics. Boldface page numbers indicate primary treatment of species of Siphonaptera.

albatross, Laysan, 33, 46
  nest, 33. *See also* Diomedea immutabilis nest, 8, 32
alexandrinus (Rattus), 21, 46
anisus (Monopsyllus), 4, 5
auropunctatus (Herpestes). *See* Herpestes auropunctatus

beaches, 8, 18
birmanicus (Herpestes), 11, 17, 46
Bos taurus, 8, 16, 18, 46
Branta sandvicensis, 8, 11, 46. *See also* nene, 11

californicus (Lophortyx), 8, 11, 46
Canis familiaris, 8, 10, 11, 13, 14, 15, 16, 17, 18, 19, 22. *See also* dog
  shed, 8. *See also* dog shed
canis
  (Ctenocephalides). *See* Ctenocephalides canis
  (*Ctenocephalus*), 4, 18, 19
  (*Pulex*), 19
cat, 10, 12, 14, 17, 18, 19. *See also* Felis catus; *F. domestica*
cattle. *See* Bos taurus, 8, 16, 18
catus (Felis). *See* Felis catus
Ceratophyllidae, 7, 8, 33
Ceratophyllus fasciatus, 33
cheopis
  (*Loemopsylla*), 20
  (*Pulex*), 20
  (Xenopsylla). *See* Xenopsylla cheopis
chicken, 10, 11. *See also* Gallus gallus, 8, 11
conditor (Leporillus), 46
Ctenocephalides
  canis, 4, 5, 7, 8, 9, 16, 18, **19**, 20; *figs. 15-18*
  felis, 4, **15**, 18
  felis felis, 7, 8, 9, **15**, 18, 19; *figs. 11-14*
  orientis, 18, 19
Ctenocephalus
  canis, 4, 18, 19
  felis, 15
Ctenopsyllus
  musculi, 35
  segnis, 36
culmorum (Rattus), 27, 46
cuniculus (Oryctolagus). *See* Oryctolagus cuniculus

Diomedea immutabilis, 46
  nest, 8, 32. *See also* albatross
dog, 10, 11, 12, 13, 14, 17, 18, 19, 20. *See also* Canis familiaris
  shed, 13, 14, 15, 19. *See also* Canis familiaris shed, 8
dog and cat flea, common, 18
dog flea, 18, 19, 20. *See also* Ctenocephalides canis
domestica (Felis), 17, 46
domesticus (Passer), 8, 11. *See also* sparrow, 10

Echidnophaga
  gallinacea, 4, 7, 8, 9, **10**, 11, 12; *figs. 2-4*. *See also* sticktight flea, 11, 14
  gallinacea gallinacea, 10

familiaris (Canis). *See* Canis familiaris
fasciata (Nosopsylla), 33
fasciatus (Nosopsyllus). *See* Nosopsyllus fasciatus
Felis
  catus, 8, 11, 16, 17, 18, 19, 36. *See also* cat
  domestica, 17, 46. *See also* cat
felis
  (Ctenocephalides). *See* Ctenocephalides felis
  (*Ctenocephalus*), 15
felis felis (Ctenocephalides). *See* Ctenocephalides felis felis
Felis (Pulex), 15

gallinacea
  (Echidnophaga). *See* Echidnophaga gallinacea
  (*Sarcopsylla*), 10
  (*Xestopsylla*), 10
gallinacea gallinacea (Echidnophaga), 10
gallinaceus (Sarcopsyllus), 10
gallus (Gallus), 8, 11. *See also* chicken, 10, 11; poultry
  buildings & yards, 8, 10, 11
goose, Hawaiian, 46
gwyni
  (Polygenis), 4
  (*Rhopalopsyllus*), 4

hawaiiensis (Rattus), 10, 21, 25, 46
  nest, 25. *See also* Rattus exulans nest

hawaiiensis (Xenopsylla). See Xenopsylla hawaiiensis; Xenopsylla vexabilis hawaiiensis
Hawaii Island, localities on:
Ahualoa, 17, 21, 25, 34, 36
Captain Cook, 14, 21
Glenwood, 14
Haina, 13, 14, 15, 26
Hakalau, 14
Halaula, 11, 17, 21
Halaula School, 14
Halawa, 14
Halepiula, 34, 36
Halepohaku, 36
Hamakua Coast, 18, 19, 21, 22
Hamakua District, 11, 13, 17, 19, 21, 23, 25, 26, 27, 29, 31, 34, 36, 37
Hanaipoe, 13, 36
Hawaii Volcanoes National Park, 26, 28, 34, 36
Hawi, 14, 15, 17, 36
Hilo, 11, 13, 14, 15, 17, 21, 25, 28, 36
Holualoa, 14
Honalo, 14
Honaunau, 14, 15, 17
Honohina, 14
Honokaa, 11, 13, 14, 15, 17, 19, 21, 22, 23, 25, 26, 34, 36, 37
Honokahau, 14
Honomu, 14, 26
Hookena, 14
Humuula, 11, 13, 14, 15, 17, 19, 20
Iolehaehae Camp (Kukaiau Ranch), 28
Kaapahu Homesteads, 26, 34
Kahaluu, 14, 17, 26
Kahawailiilii Gulch, 34, 36
Kahua Ranch, 13
Kailua, 14
Kaimu, 14, 17
Kainaliu, 14
Ka Lae, 22
Kalapana, 14
Kalopa, 11, 17, 21, 25, 34, 36
Kalopa Gulch, 26
Kamuela, 13, 14, 15, 17, 28. *See also* Waimea, 11
Kapaau, 14, 17
Kapoho, 14
Kapulena, 13, 14, 26, 34, 36
Kaumana, 14, 17, 19
Kaunamano Gulch, 21, 25, 36
Kawaihae, 11, 12, 14, 15, 17, 18, 22
Keaau. *See* Olaa
Kealakekua, 14
Kealia, 14
Keanakolu, 17, 34, 36
Keauhou, 14
Keauhou Ranch, 14
Keaukaha, 14
Kilauea Military Camp, 14, 34, 36
Kohala Mill, 14, 17, 26
Kohala Mountain, 28, 34, 36
Kukaiau, 11, 14, 17, 21, 25, 34, 35, 36
Kukaiau Ranch, 11, 17, 18, 26, 28, 34, 36
Kukuihaele, 11, 13, 14, 15, 17, 21, 22, 25, 26, 29, 30, 34, 35, 36, 37
Kupaahu, 14, 22
Kurtistown, 14
Laupahoehoe, 14, 17, 21, 25, 28, 34
Lower Pohakea, 11, 17, 21, 25, 34, 36
Mahukona, 14, 17, 22
Makahalau, 14, 22
Makahalau Camp, 11, 17, 22, 34, 36
Makapala, 14, 22
Mana, 34, 36
Milolii, 14
Mountain View, 14, 15, 17
Naalehu, 14
Napoopoo, 11, 14, 15, 17, 36
Ninole, 14
Niulii, 11, 14, 15, 17
North Kohala District, 17
North Kona District, 28
Olaa, 11, 14, 17, 21, 25, 28, 34, 35, 36, 37
Onomea, 11, 12, 14, 15, 17, 21
Ookala, 13, 14, 15, 17, 26
Paauhau, 14, 15, 21, 25, 26, 28
Paauilo, 13, 14, 15, 17, 22, 34, 35, 36, 37
Pahala, 14
Pahoa, 14, 17
Palihooukapapa, 17, 34, 36
Papaaloa, 14
Papaikou, 14, 17
Parker Ranch, 15
Pepeekeo, 14, 21, 25
Piihonua, 14, 15
Pohakea Ranch, 14
Pohakuloa, 11, 13, 14, 15, 34, 35, 36, 37
Pohoiki, 14
Pololu Valley, 23, 26
Puako, 11, 14, 15, 17
Puna District, 17
Punaluu, 14, 17
Puu Keanui, 34, 36
Puu Kihe, 11, 12, 18, 34, 35, 36
Puu Laau, 13
Puu Mali, 18
Puu Waawaa Ranch, 13, 14, 22, 26, 34, 37
Puuanahulu, 13, 14, 15, 18, 22, 36
South Cape. *See* Ka Lae, 22
South Hilo District, 11, 17, 34, 36
South Kona District, 17
Umikoa, 11, 13, 14, 18, 34, 37
Upolu Point, 22
Upper Pohakea, 17, 25, 28, 34, 36

Waiakea Camp No. 6, 14
Waiakeauka, 18
Waikii, 11, 14, 18, 37
Waimea, 11. *See also* Kamuela
Wainaia Gulch, 22, 26
Waiohinu, 14, 18
Waipio, 17, 22
Waipio Valley, 14, 17, 18, 22, 26, 28
Wood Valley, 14

Hawaiian rat flea, 26. *See also* Xenopsylla vexabilis
Herpestes
auropunctatus, 8, 11, 13, 15, 16, 17, 18, 21, 22, 26, 34, 35, 36, 37, 46. *See also* mongoose
den, 8, *See also* mongoose den, 17, 18
birmanicus, 11, 17, 46
Homo sapiens, 8, 15, 16, 18, 19, 22, 26. *See also* man, 14, 18, 21
houses & yards, 8, 13, 14, 16, 18, 19, 21, 22, 26
human flea, 13, 14, 18. *See also* Pulex irritans

immutabilis (Diomedea), 46. *See also* Diomedea immutabilis nest, 8, 32; albatross
irritans (Pulex), 12. *See also* Pulex irritans; human flea

jonesi (Leporillus), 27, 46

Kauai, localities on:
Haena, 10, 14, 16
Hanapepe, 10, 16
Kalaheo, 16
Kaumakani, 15
Kawaihau District, 21, 25
Kilauea, 16
Kipu, 16
Kokee, 15, 16, 36
Koloa, 16
Koloa District, 21, 25
Lawai, 16
Lihue, 16
Makaweli, 16
Omao, 16
Puhi, 16
Wailua, 15, 16
Waimea District, 10, 16, 21, 25, 36

Lanai, locality on:
Lanai City, 17
Laysan, locality on, 32, 33
laysanensis Wilson, n. sp. (Parapsyllus), 5, 7, 8, 9, 31, 33; *figs. 28-31, 33*
Leporillus
conditor, 46
jonesi, 27, 46
Leptopsylla
musculi, 35
segnis, 7, 8, 9, 30, 34, 35, 36, 37; *figs. 38-40*
Leptopsyllidae, 7, 8, 35
Loemopsylla cheopis, 20
longicornis group (Parapsyllus), 31
Lophortyx californicus, 8, 11. *See also* California quail, 12

man, 14, 18, 21, 23, 31. *See also* Homo sapiens
Manana Island, locality on, 4, 11, 17, 19, 21, 23
Maui, localities on:
central Maui, 17, 21, 23, 25, 28, 37
Haiku, 11, 17, 21, 25, 33, 36
Haleakala Crater, 11, 17
Haleakala National Park, 36
Kaheka area, 17
Kahului, 11, 21, 25, 28, 33, 36
Kailua, 11, 17, 21, 25, 33, 36
Keokea, 11, 17, 21
Kihei, 11, 17
Kipahulu Valley, 33
Kula, 11, 17, 21, 25, 33, 36
Kula area, 11, 17, 23, 28, 33, 35, 36, 37
Lahaina, 11
Lahaina area, 17, 21
Lower Paia, 11, 17, 21, 25, 33, 36
Makawao, 11, 17, 21, 25, 33, 36
Makawao District, 11, 17, 21, 25
Olinda, 11, 17, 21, 25, 33, 36
Paia. *See* Upper Paia
Puunene, 11, 17, 21, 25, 28, 33
Upper Paia, 11, 17, 21, 25, 33, 36
Waiakoa, 17
Wailuku, 11, 17, 21, 25
Molokai, localities on:
Honomuni, 17
Hoolehua, 17
Kaunakakai, 11, 17
Maunaloa, 17
McVeigh's cabin, 17
Waikolu Valley, 17
mongoose, 10, 12, 13, 14, 16, 17, 19, 21, 31, 36, 37. *See also* Herpestes auropunctatus
den, 17, 18. *See also* Herpestes auropunctatus den, 8
Monopsyllus anisus, 4, 5
mouse, house, 12, 19, 23, 35, 36, 37. *See also* Mus musculus
nest, 29. *See also* Mus musculus nest

mouse flea, 37. *See also* Leptopsylla segnis
murine typhus, 34
musculi
(*Ctenopsyllus*), 35
(*Leptopsylla*), 35
Mus musculus, 8, 11, 12, 18, 21, 22, 25, 26, 28, 30, 34, 35, 36, 37. *See also* mouse
nest, 8, 22, 25, 26, 29, 30, 36, 37

nene, 11, 46. *See also* Branta sandvicensis, 8, 11
nesiotes (Xenopsylla), 27
northern rat flea, 34, 35. *See also* Nosopsyllus fasciatus
norvegicus (Rattus). *See* Rattus norvegicus
Nosopsylla fasciata, 33
Nosopsyllus
(*Ceratophyllus*) *fasciatus*, 33
fasciatus, 7, 8, 9, **33**, 34, 35, 37; *figs. 35-37*

Oahu, localities on:
Aiea, 10, 16, 21, 25
Ewa Beach, 16
Hickam Air Force Base, 16
Honolulu, 4, 10, 11, 13, 14, 16, 18, 19, 21, 22, 25, 33, 36
Kailua, 10, 16
Kaneohe, 16
Kaneohe Marine Corps Air Station, 16
Kipapa, 10, 16, 21, 25
Koko Head, 10, 16
Manoa Valley, 11, 16, 21
Pali, 25
Red Hill Navy Reservation, 16
Tantalus, 16, 21
Wahiaivu, 21
Wahiawa, 21
Waimanalo, 10, 16, 21, 25
Waipahu, 10, 16, 21, 25
Oriental rat flea, 22, 23. *See also* Xenopsylla cheopis
Oriental-Pacific rat flea, 26. *See also* Xenopsylla vexabilis
orientis (Ctenocephalides), 18, 19
Oryctolagus cuniculus, 8, 11, 17, 18, 21, 22. *See also* rabbit, 4, 19

pacificus (Puffinus), 32, 33, 46
nest, 8, 32
Parapsyllus, 33
laysanensis Wilson, n. sp., 5, 7, 8, 9, **31**, 33; *figs. 28-31, 33*
longicornis group, 31
taylori, 33; *figs. 32, 34*
Passer domesticus, 8, 11, 46. *See also* English sparrow, 10
nest, 8, 11. *see also* sparrow nest, 10
Pasteurella pestis. *See* Yersinia pestis, 31; plague
pig, 12, 14. *See also* Sus scrofa, 8, 11, 13, 15
plague, 4, 12, 22, 23, 25, 28, 31. *See also* Yersinia pestis, 31
Polygenis gwyni, 4
poultry, 11, 12. *See also* chicken
buildings, roosts & yards, 8, 10, 11
Puffinus, 33
pacificus, 32, 33, 46
nest, 8, 32, 33
tenuirostris, 46, 69
spp., 33
Pulex
canis, 19
cheopis, 20
fasciatus, 33
Felis, 15
irritans, 4, 7, 8, 9, **12**, 13, 14, 15; *figs. 5-9*. *See also* human flea, 13, 18
segnis, 35
serraticeps, 18, 19
simulans, 4, 7, 8, 9, 13, **14**, 15; *fig. 10*
sp., 7, 8, **15**
Pulicidae, 7, 8, 10

quail, California, 12. *See also* Lophortyx californicus, 8, 11

rabbit, European, 4, 19. *See also* Oryctolagus cuniculus
rat, 10, 11, 12, 13, 14, 16, 17, 21, 22, 23, 25, 27, 28, 30, 31, 33, 34, 35, 36. *See also* Rattus
black, 46. *See also* Rattus rattus
brown, 21, 46. *See also* Rattus norvegicus
Hawaiian, 21, 26, 46. *See also* Rattus exulans
Norway, 21, 23, 25, 26, 46. *See also* Rattus norvegicus
Polynesian, 46. *See also* Rattus exulans
roof, 46. *See also* Rattus rattus
stick-nest, 46
Tunney's, 46
Rattus
alexandrinus, 21, 46
culmorum, 27, 46
exulans, 4, 5, 8, 10, 11, 16, 17, 18, 21, 22, 23, 25, 26, 27, 28, 29, 30, 33, 34, 35, 36, 37, 46
nest, 8, 17, 18, 22, 25, 26, 29, 30, 34, 35, 36, 37
hawaiiensis, 10, 21, 25, 46
nest, 25
norvegicus, 4, 8, 10, 11, 12, 16, 18, 19, 21, 22, 23, 25, 26, 28, 34, 35, 36, 37, 46
nest 8, 22, 25, 26, 34, 36, 37

rattus, 4, 8, 10, 11, 16, 18, 21, 22, 23, 25, 26, 28, 34, 35, 36, 37, 46
nest, 8, 25, 26
tunneyi, 46
sp., 17, 21, 25, 33, 36
Rhopalopsyllidae, 7, 8, 31
Rhopalopsyllus gwyni, 4
rodents, 17, 19, 21, 22, 25, 26, 30, 34, 36, 37. *See also* Mus musculus; Rattus

sandvicensis (Branta), 8, 11, 46. *See also* nene, 11
sapiens (Homo), 8, 15, 16, 18, 19, 22, 26. *See also* man, 14, 18, 21
Sarcopsylla gallinacea, 10
Sarcopsyllus gallinaceus, 10
scrofa (Sus). *See* Sus scrofa; pig
sea birds, 33
segnis
(Leptopsylla). *See* Leptopsylla segnis
(*Pulex*), 35
serraticeps (Pulex), 18, 19
shearwater, short-tailed, 46. *See also* Puffinus tenuirostris, 69
simulans (Pulex). *See* Pulex simulans
sparrow, English or house, 10. *See also* Passer domesticus
sticktight flea, 11, 14. *See also* Echidnophaga gallinacea, 7, 8, 9, **10**, 11, 12
Sus scrofa, 8, 11, 13, 15. *See also* pig

taurus (Bos), 8, 16, 18, 46
taylori (Parapsyllus), 33; *figs. 32, 34*
tenuirostris (Puffinus), 46, 69
tunneyi (Rattus), 46
typhus, murine, 34

vexabilis (Xenopsylla). *See* Xenopsylla vexabilis
vexabilis hawaiiensis (Xenopsylla), 24, 25, 27. *See also* Xenopsylla vexabilis

Xenopsylla
cheopis, 4, 7, 8, 9, **20**, 22, 23, 25, 26, 31; *figs. 19-22*
hawaiiensis, 23, 24, 27
nesiotes, 27
vexabilis, 4, 5, 7, 8, 9, 22, **23**, 24, 25, 26, 27, 28, 29, 30, 31; *figs. 23-27*
vexabilis hawaiiensis, 24, 25, 27
Xestopsylla gallinacea, 10

Yersinia pestis, 31. *See also* plague, 4, 12, 22, 23, 25, 28, 31